Primary production of intertidal marine macroalgae: factors influencing primary production over wide spatial and temporal scales

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Abstract

Oxygenic photosynthesis is responsible for virtually all of the biochemical production of organic matter in both marine and terrestrial ecosystems. Despite the large amount of research on phytoplankton, macroalgae have received less attention despite them being, on a per-area basis, one of the most productive ecosystems on earth. Furthermore, there has been a tendency of studies to measure primary production in single thalli, or monospecific stands. The lack of studies examining *in situ* production of whole assemblages using photorespirometry, as is common practice in soft-sediment systems, may be related to a lack of suitable apparatus. This research aimed to develop unique techniques and an apparatus for measuring primary production of intact macroalgal assemblages in laboratory and field conditions. Photorespirometry chambers were developed and tested on *in situ* macroalgal assemblages, giving information on the role of species identity, biodiversity, irradiance and community structure on overall primary production. Furthermore, the successful application of these methods was used to model annual primary production over local and regional scales, as well as the potential effects of human disturbance on production.

In this study, photosynthesis-irradiance relationships (P-E curves) of intact intertidal algal assemblages showed no signs of saturation at high irradiance levels, as is typically seen in single species curves. Furthermore, diverse macroalgal assemblages showed a two-stage rise in production, with a significant enhancement of production at high irradiance. Evidence from this study suggests that the three-dimensional structure of natural assemblages, functional diversity and their interaction with a complex light environment is responsible for the unique P-E curves. The increased efficiency of light use in complex assemblages suggests an important role of species complmentarity in enhancing production with species diversity. This research also shows the potential consequences of disturbance on macroalgal assemblages, with the loss of several species causing a major decline in net production. The methods developed in this thesis have allowed simple modelling of annual rates of primary production and the parameters driving production of macroalgae over long time-scales. Respiration rates have a particularly large influence on production models and indicate that increasing temperature due to climate change could have significant consequences for net carbon fixation of macroalgae.

This research gives valuable insight into the production of marine macroalgae and reinforces the notion that they are amongst the most productive systems on earth. These results revealed the importance of examining natural communities, as opposed to randomised assemblages and suggest a vital role of species diversity and community composition. Although there was no functional redundancy of the canopy forming species there did appear to be significant redundancy within the subcanopy assemblage. The identity of subcanopy species had little effect on production, but over longer temporal scales, as species come and go, they may help buffer the communities in terms of primary production. Furthermore, the relationship between biodiversity and ecosystem function (primary production), although driven by diversity, is moderated by resource levels. The complex relationship between irradiance, diversity and production shows the importance of resource levels in the enhancement of function with increasing biodiversity. Due to fundamental differences in terrestrial and marine systems, I was able to examine the effects of discrete levels of irradiance on production, which indicated an important role of complementary light use. This study represents advancements not only in the understanding of primary production in macroalgal assemblages, but also has implications for how diversity may enhance function in other autotrophic systems. The important role of enhanced efficiency of photon capture in multi-canopy layer communities may prove an essential process in ecosystems as diverse as macroalgal beds and tropical rain-forests.

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Introduction

Primary production of marine macroalgae

1.1. Introduction

Oxygenic photosynthesis is responsible for virtually all of the biochemical production of organic matter in both marine and terrestrial ecosystems. The transfer of energy through most food webs can be directly linked to the fixation of carbon dioxide at the primary producer level (Field et al. 1998). Changes in the magnitude of carbon fixed through primary production can strongly influence atmospheric CO_2 levels and hence the climate over geological time scales (Falkowski et al. 1998). Therefore, any major alteration in carbon fixation through primary production could have severe consequences on the functioning of ecosystems, as well as on the functioning of global biogeochemical cycles (Falkowski et al. 1998). Anthropogenic-driven changes in climate and biogeochemical systems could threaten the rate and quantity of carbon fixed by photoautotrophs with potentially catastrophic consequences. In particular, the global carbon cycle is being altered directly by changes in carbon fluxes, such as through fossil fuel burning, and indirectly through changes in atmospheric chemistry, especially increases in green house gases (Geider et al. 2001). Quantifying current rates of carbon fixation is paramount if we are to understand the potential impacts of climate change or anthropogenic disturbance on primary producers and the biogeochemical cycles that they regulate.

At the global scale, terrestrial net primary production (NPP) is one of the most-modelled ecological parameters (Field et al. 1995). NPP can be defined as either increases in biomass or CO_2 exchange (Field et al. 1995). When considered as CO_2 exchange, NPP can be defined by the equation:

$$\mathbf{NPP = GPP - R_a}$$

Where GPP (Gross Primary Production) is the total carbon fixed by photosynthesis and R_a is autotrophic respiration. The production rate of any plant biomass is determined by the size of the plant biomass and the amount of radiant energy impinging onto that biomass (Antoine & Morel 1996). NPP is sensitive to many other factors, including climate, available nutrients, and disturbance regimes (Field et al. 1995; Cramer et al. 1999). Although these influences on NPP have been extensively studied, the ecological interactions that determine community structure and, in turn, influence NPP have been largely ignored (Geider et al. 2001). The interactions between species within assemblages are often neglected in studies of primary production, particularly in satellite imagery models which may overlook the NPP of subcanopy species. Studies in terrestrial forest ecosystems indicate that the subcanopy assemblage can contribute up to 30% of total

primary production (Williams et al. 1997; Mission et al. 2007), yet many wide scale studies consider production of only the canopy (Field et al. 1998). The role of species interactions on primary production has the potential to give valuable insight into global models of primary production, as well as into the potential role of biodiversity on ecosystem function.

Marine Primary production

Current estimations of oceanic primary production suggest that it accounts for approximately 49% of the global total (Field et al. 1998). A large majority of primary production research within oceanic systems has focused on pelagic phytoplankton, which play an essential role in global carbon sequestration (Falkowski et al. 1998). The biological carbon pump, the process by which phytoplankton absorb CO_2 from the surface waters by photosynthesis and store it in benthic sediments after they die and sink, is considered a very important mechanism in the regulation of the earth's climate (Falkowski et al. 2000; Geider et al. 2001). Despite the large amount of attention on microalgae (phytoplankton in particular), macroalgae have received less attention. Macroalgae exist in shallow water surrounding land masses, a relatively small area compared to terrestrial and oceanic ecosystems, but this thin band accounts for approximately 1% of global primary production (Field et al. 1998). Although this seems relatively insignificant, on a per-area basis this one of the most productive regions on earth (Mann 1972; Mann 1973; Field et al. 1998).

Although marine macrophytes make up a small proportion of ocean primary production, they undoubtedly supply a majority of the biomass to nearshore ecosystems. Macroalgal subsidies are documented in analyses of stable isotopes, which indicate that the signature of marine algae extends far beyond areas where they occur, including non-vegetated nearshore areas and terrestrial landscapes (Anderson & Polis 1998; Hyndes & Lavery 2005), intertidal mud flats (Riera & Hubas 2003), offshore communities (Hill et al. 2006), and deep offshore basins (Fischer & Wiencke 1992). Given this significant contribution to production, it is perhaps surprising that relatively little is known about the contribution of marine macroalgae to total primary production. Several models have estimated production of macroalgae, but the methods used and the results vary widely, both within and among species (Jackson 1977; Ferreira & Ramos 1989; Duarte & Ferreira 1997; Reed et al. 2008). For example, estimates of production for *Macrocystis pyrifera*

vary from 0.42- 3.2 kg C m^{-2} yr^{-1} within and between authors (Jackson 1977; Reed et al. 2008). Production estimates of macroalgal species, including laminarian and fucoid species range between 0.07- 3.2 kg C m^{-2} yr^{-1} (Jackson 1977; Ferreira & Ramos 1989; Duarte & Ferreira 1997; Reed et al 2008). This variation within and between macroalgal species could be due to a wide range of differences between sites, changes in assemblage density over time and different methods of converting measurments into aereal production. The dynamic nature of macroalgal assemblages has the potential to contribute to very different predictions of primary production (Dayton et al. 1992; Schiel & Lilley 2007). Therefore, determining macroalgal production will involve very different methods and techniques compared to terrestrial ecosystems.

Measuring primary production in the marine environment has its own set of challenges and nuances compared to terrestrial ecosystems, but may offer insight into dynamics of production which are difficult to determine in terrestrial systems. For example, because of the physical properties of water, marine macroalgae require much less structure (i.e., rigid tissue to maintain vertical position) than terrestrial plants; this makes estimations of net primary production much simpler because of the relative lack of tissue specialisation and all macroalgal tissue is potentially photosynthesising (although not all tissues photosynthesize equally, i.e., holdfasts; Lobban et al. 1985). The relatively small sizes of many macroalgal assemblages compared to analogous terrestrial ecosystems means they could potentially be isolated to test whole assemblage production with gas exchange measurements. This may provide valuable information on the relative roles of species identity and species diversity in their contributions to primary production within whole assemblages.

Losses or reductions in the abundance of primary producers have the potential to alter the quantity of carbon fixation (Chapin et al. 2000). There is relatively little information regarding the potential consequences of macroalgal species loss (or declining abundance) on ecosystem functioning, particularly primary production. However, research that has been done indicates that macroalgal diversity enhances primary production (Bruno et al. 2005) and nitrogen uptake (Bracken & Stachowicz 2006; Bracken et al. 2008). Loss of macroalgal species could have a significant impact on the stability of nearshore ecosystems, and may have consequences reaching beyond the nearshore marine environment. Furthermore, there may be very little functional replacement of canopy forming macroalgae (Schiel 2006). Although studies testing the effects of random species loss are prolific, very few studies have tested the effects of non-

random species loss in real communities (Naeem 2006; Stachowicz et al. 2007; Bracken et al. 2008). Understanding the effects of macroalgal species loss from real ecosystems is essential if we are to understand the potential threats to primary production in nearshore ecosystems and the consequences of reductions in biomass output (Naeem 2006).

Production-irradiance curves

To fully understand primary production of macroalgae it is essential to understand how they respond to irradiance (Middleboe & Binzer 2004). Production-irradiance (P-E) curves are frequently used to describe the changes in production with increasing irradiance (Webb et al. 1974; MacIntyre et al. 2002; Middleboe & Binzer 2004; Binzer & Middleboe 2005). These curves generally fit the common saturation curve as described by Webb et al. (1974) and with the addition of a photoinhibition factor or β (Walsby 1997) described by the equation:

$$P_c = P_m[1 - \exp(-\alpha E/P_m)] + R + \beta E$$

Where P_c describes the curve of production at a given irradiance level, P_m is maximum production, α is the slope at non-saturating irradiance, E is irradiance, R is the respiration rate at zero irradiance, and β is the negative slope caused by photoinhibition at high irradiance. Also, the irradiance at compensation E_c, where production and respiration are equal (i.e., y = 0) and the irradiance at saturation E_k are also important parameters which describe the P-E curve. All of these photosynthetic parameters are illustrated on Fig. 1.1.

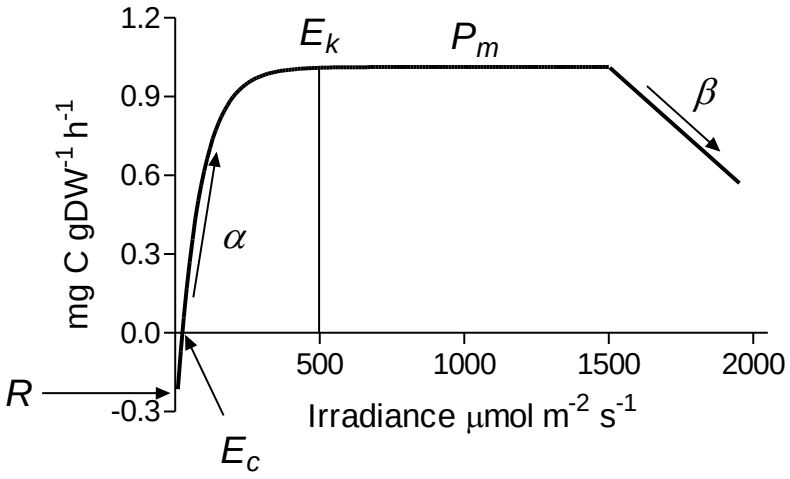

Figure 1.1. Diagrammatic representation of commonly measured photosynthetic parameters and how they relate to a typical P-E curve.

Although a large amount of research has described the relationship between production and irradiance in many autotrophic species (Webb et al 1974; Walsby 1997), recent evidence suggests that typical saturation curves may not always be relevant in real assemblages (Middleboe & Binzer 2004; Binzer & Middleboe 2005). In complex, naturally structured assemblages, saturation of photosynthesis does not occur until very high irradiance levels, and sometimes, does not occur at all (Middleboe & Binzer 2004). Therefore, studies attempting to define production by assuming a saturating level of irradiance in complex assemblages (i.e., Golléty et al. 2008) may be confounding results by assuming a constant level of production beyond low levels of irradiance. Therefore, in order to understand more complex processes, such as the effects of disturbance and the role of diversity, production needs to be tested across a range of irradiance levels. Research on the role of diversity on ecosystem function indicates that resource levels moderate the role of diversity on ecosystem function (Fridley 2002; Tylianakis et al. 2008). Understanding whether light drives the relationship between biodiversity and ecosystem function in macroalgal assemblages may indicate the circumstances under which diversity enhances function and the mechanisms operating.

Biodiversity and ecosystem function

The role of biodiversity in maintaining ecological stability has been questioned by ecologists for over half a century (Odum 1953). May (1973) showed that the stability of ecosystems was dependent on species diversity with the loss of diversity negatively affecting ecosystem stability. These early debates have led to further speculation on the relationship between diversity and the functioning of ecosystems (Ehrlich & Ehrlich 1981) and a renewed interest in the consequences of biodiversity loss. Ecosystem function can be defined by a range of processes, including primary production, biomass accumulation, decomposition rates, nutrient use, bioturbation, just to name a few (Schwartz et al. 2000). Research in the early 1990s on the consequences of changing biodiversity on various types of "ecosystem functions" led to both great insights and debates (Vitousek & Hooper 1993; Naeem et al. 1994; Tilman & Downing 1994, Tilman 1996; Huston 1997; Naeem and Li 1997; Tilman et al. 1997). The insights of this early research were that species diversity does enhance function, but there was, and continues to be, a large debate surrounding the mechanisms enhancing function (Loreau & Hector 2001). Since these studies, research on the effects of biodiversity on ecosystem function

(termed 'BEF') has become prolific, motivated primarily by increasing rates of species loss and the transferral of species worldwide (Ruiz et al. 2000; Brown & Sax 2004). Expansion of this field is understandable, given the potential impacts humans have on ecosystems. Indeed, it makes intuitive sense that as species are lost from ecosystems, their roles and the services they provide maybe lost or diminished and critical pathways could be affected, to the detriment of communities or the wider ecosystem (Naeem & Wright 2003). Understanding how the loss of a species or functional group affects the functioning of the wider ecosystem is vital if we are to lessen or mitigate the impacts of anthropogenic disturbance.

There are many possible ways the loss of a species may influence a given ecosystem function (Schwartz et al. 2000), but these can be condensed into three main hypotheses, these are: (1) redundancy, which implies that species can be substituted and the loss of a species can be compensated for by another; (2) species are singular, making unique contributions to an ecosystem (otherwise known as the 'rivet hypothesis'); and (3) the role of species is context-dependent and the effects of species loss are individualistic and unpredictable (Lawton 1994; Peterson et al 1998; Naeem et al. 2002). Most of the hypotheses are shown by Fig 1.2., which shows the potential relationship between diversity and ecosystem function (Schwartz et al. 2000). The likelihood of a redundancy scenario in nature is debated (Loreau 2004), with redundancy being incompatible with stable co-existence as predicted by classical Lokta-Volterra models of competition. Furthermore, the presence of complementarity is contrary to functional redundancy, with the two unlikely to occur simultaneously (Loreau 2004). The effects of species loss on ecosystem processes is relevant to conservation efforts, with the redundant species hypothesis giving hope that ecosystems may have the capacity to buffer species loss to some degree. However, nature is neither compliant nor simple, and the actual effects of species loss may be a combination of all three hypotheses. For example, there may be singularity in some structural components such as canopies (e.g., Lilley & Schiel 2006), but redundancy in others, such as the understory. Furthermore, there is some evidence that another hypothesis is also necessary to explain the impacts of species loss, and that is a 'key' or 'keystone' hypothesis, where the loss of a single species has a greater than predicted impact on ecosystem function (Paine 1974; Bruno et al 2003; Schiel 2006). This hypothesis may be particularly relevant for ecosystem engineers, which provide multiple services to ecosystems and in certain cases, have no functional equivalents (Schiel 2006).

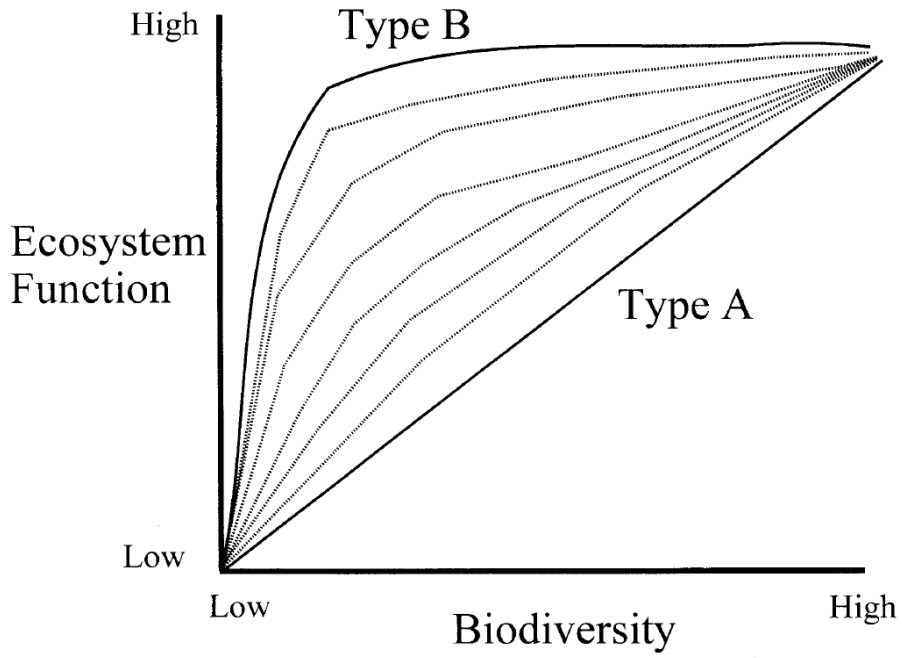

Figure 1.2. The role of species diversity on a given ecosystem process (e.g., primary production). This figure shows the two main hypotheses, type A where each species, even the very rare, contribute to function and type B where there is a large amount of functional redundancy and a continuum of relationships between the two hypotheses (figure from Schwartz et al. 2000).

Probably the most measured function of ecosystems is primary production (Loreau et al. 2001), which is not surprising given that almost all organic matter in ecosystem can be traced to carbon fixed at the primary producer level. The relationship between biodiversity and primary production has been intensely debated, particularly in regard to whether community diversity depends on production (Grime 1979; Huston 1979), or production depends on diversity (Vitousek & Hooper 1993; Naeem et al. 1994). Regardless of whether production drives, or is driven by diversity, many studies indicate an enhancement of primary production with increasing plant diversity (Loreau et al. 2001). However, one of the major debates in BEF research has been the relative contribution of 'selection effects' and 'complementarity effects' to the enhancement of production (Loreau 1998a). In the 'selection effect', dominance by species with particular traits, such as high production or biomass which disproportionately affect ecosystem processes, whereas in the `complementarity effect', resource partitioning among species or positive interactions lead to increased total resource use (Loreau & Hector 2001). The mechanisms by which ecosystem function is potentially enhanced with increasing

diversity are illustrated below (Fig. 1.3). Initially, complementarity was suggested to enhance production in many systems, but much of the evidence suggested that selection effects were more common (Loreau et al. 2001). However, increasing evidence suggests that complementarity may be more important in the enhancement of function with diversity (Spehn et al. 2005), particularly in experiments over longer temporal scales (Cardinale et al. 2007; Fargione et al. 2007; Marquard et al. 2009). The role of complementarity may become increasingly important when studies on natural assemblages, as opposed to experimental assemblages, become more prevalent.

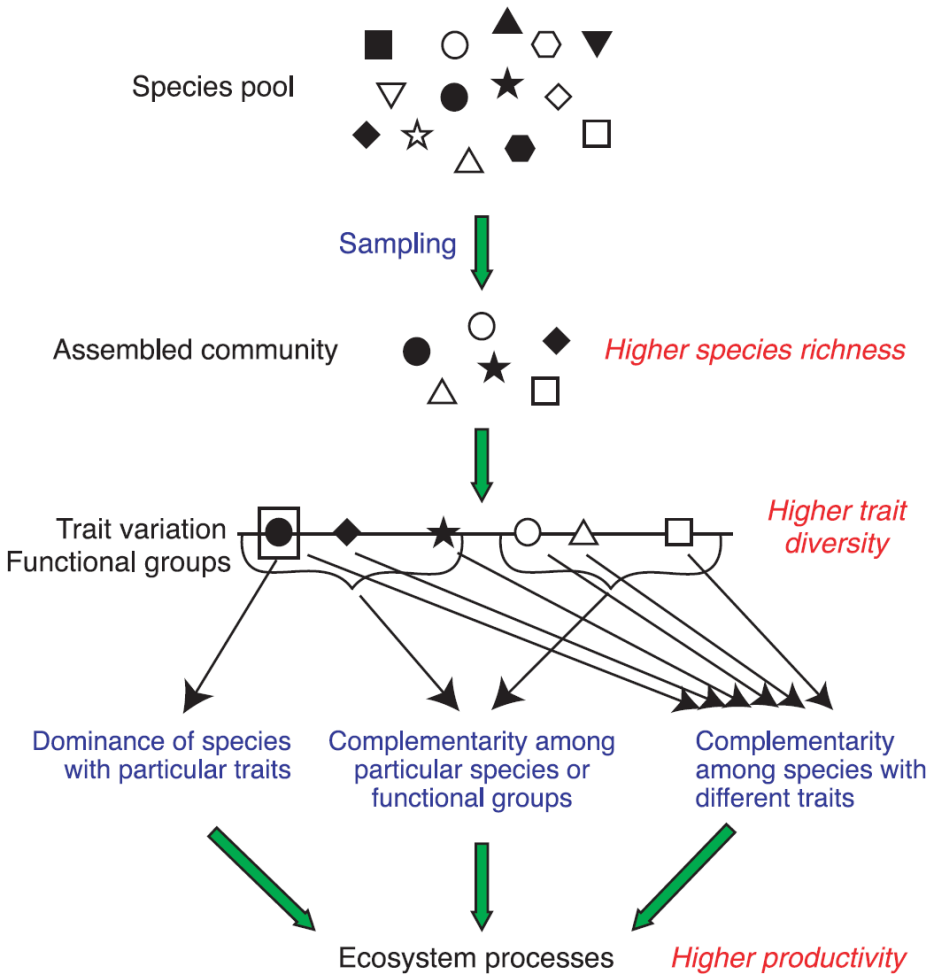

Figure 1.3. The contribution of sampling effects and complementarity on ecosystem processes in experiments testing the role of biodiversity on ecosystem function (from Loreau et al 2001).

Biodiversity ecosystem function in the marine environment

Although much evidence points to an enhancement of function with diversity in the terrestrial environment, the marine environment remains largely enigmatic due to its large size and taxonomic complexity (Worm et al. 2006). Ecosystems that encompass estuaries (Lotze et al. 2006), coral reefs (Pandolfi et al. 2003) and coastal fisheries (Jackson et al 2001) are rapidly losing populations, species or entire functional groups, largely due to anthropogenic effects (Pauly et al. 1998; Dulvy et al. 2003; Worm et al. 2006). Despite the large amount of interest in the role of biodiversity in enhancing ecosystem function, marine studies have lagged considerably behind terrestrial research (Naeem 2006). Furthermore, many of the studies have focused on higher trophic levels such as grazers (Duffy et al. 2001), or infaunal invertebrate assemblages (Emmerson et al 2001; Solan et al. 2004), with only a handful of studies testing primary production of macroalgae or proxies of production (Bruno et al. 2005; Bracken et al. 2008). Research on higher trophic levels provides an essential contrast to research on terrestrial ecosystems (Duffy 2009), but the lack of research on marine primary producers makes drawing larger inferences about the relationship between plant diversity and production difficult. Current research suggests that macroalgal diversity enhances primary production, but this is largely due to selection effects (Bruno et al. 2005). However, growing evidence suggests that natural macroalgal assemblage structure may be important in uncovering the relationship between biodiversity and production (Bracken et al. 2008; Stachowicz et al. 2008). A better understanding of the relative role of complementarity in macroalgal assemblages is essential in exploring the role of diversity and the potential impacts of species loss in marine communities.

Complementarity in the use of total nitrogen (NO_3^- and NH_4^+) has been shown to be enhanced by macroalgal diversity (Bracken et al. 2008). Although nitrogen is one of the most important nutrients for macroalgal growth, other resources, particularly light, may be partitioned among species. The role of species diversity in complementary light use has been tested in terrestrial grassland communities, and although there appears to be some complementary resource use, parsing the effects of above-ground and below-ground resource use is difficult (Yachi & Loreau 2007; Vojtech et al. 2008). The lack of root structure and specialisation, as well as the relatively small size of macroalgal assemblages (compared to terrestrial forests) makes them amenable to studies investigating the role of complementarity in whole assemblages.

1.2 Objectives and aims

The aim of this study is to examine and quantify primary production of intertidal macroalgal assemblages. This research aimed to develop unique and effective means of measuring primary production of intact macroalgal assemblages in laboratory and field conditions. Methods to test production of macroalgal assemblages were then used to analyse the role of species identity, biodiversity and community structure on overall primary production. Furthermore, the successful application of these methods was used to model annual primary production over local and regional scales, as well as the potential effects of human disturbance on production. This work, therefore, encompasses a range of spatial and temporal scales, as well as selected perturbations to assemblage structure.

Chapter 2: Examines the dynamics of production in single species (thalli and monocultures) compared to multi-species intertidal assemblages under laboratory conditions. The effects of canopy structure on the primary production of intact and manipulated assemblages are examined, as well as the consequences of removing various functional groups.

Chapter 3: Develops, tests and applies a photorespirometry apparatus to *in situ* macroalgal assemblages. *In situ* measurements of primary production are compared to laboratory based measurements.

Chapter 4: Examines the role of community structure and light delivery to *in situ* macroalgal assemblages, and tests the role of functional diversity on primary production. The light use dynamics within assemblages are considered, and the irradiance environment above and below the macroalgal canopy is tested. Furthermore, the relative contributions of selection effects and complementarity are examined.

Chapter 5: Tests the effects of disturbance on primary production of macroalgal assemblages. The effects of removing canopy and subcanopy species are tested over short and long temporal scales, and the trajectory of community recovery is followed. Furthermore, the effects of canopy removal are tested along a gradient of physical stress or shore height.

Chapter 6: Uses old macroalgal canopy removal treatments (chrono-series) to test the role of disturbance on production over time scales exceeding 4 years. This was done in

intertidal assemblages at two shore-heights, examining both production and community composition.

Chapter 7: Uses *in situ* analysis of macroalgal assemblage production to model whole-reef primary production annually. Furthermore, differences in production due to temperature is used to test the potential effects of anthropogenic disturbance on annual rates of primary production.

Chapter 8: Provides an overview and synthesis of the dynamics of production in macroalgal assemblages and its implications for biodiversity ecosystem function research.

1.3 Study systems

1.3.1. *The intertidal zone of south-eastern New Zealand*

Unlike the nearshore marine systems of many other countries, the east coast of New Zealand's South Island has a high proportion of its marine macroalgal biomass within the intertidal zone. Large offshore gravel beds and highly sedimented nearshore regions in many areas, result in large areas of intertidal reef dominated by macroalgae with only patch reefs of macroalgae offshore. Furthermore, the large and conspicuous bull kelp, *Durvillaea antarctica* dominates the intertidal/subtidal fringe of semi-exposed to exposed shores in southern New Zealand, and is likely to contribute significantly to nearshore production. Although considerably smaller in size as individuals, *Hormosira banksii* forms dense beds on sheltered and semi-exposed shores in the mid shore zone (Morton & Miller 1968). The low-shore zone of the same shores is often dominated by *Cystophora* species, predominantly *Cystophora torulosa*, while the immediate subtidal zone is often dominated by a mixture of *Cystophora* species (*C. torulosa* and *C. scalaris*) and *Carpophyllum maschalocarpum*. The branching geniculate coralline alga *Corallina officinalis* is ubiquitous from the mid-shore downwards at all exposure levels, and is often beneath the canopy of dominant fucoids such as *H. banksii* and *D. antarctica*. Unlike many other intertidal systems, the east coast of New Zealand's South Island is dominated by seaweeds, particularly fucoids, with very few areas dominated by sessile invertebrates.

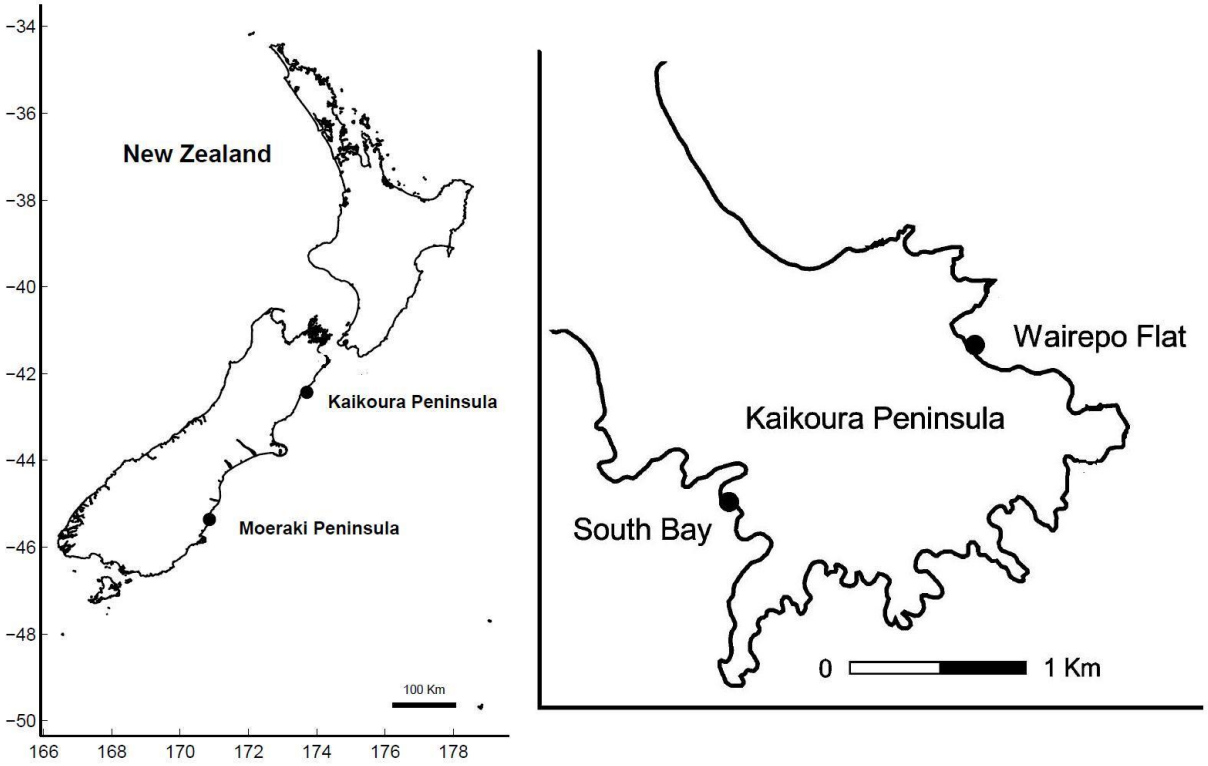

Figure 1.4. Map showing the South Island of New Zealand and the two study sites Moeraki and Kaikoura. Expanded view of the Kaikoura peninsula shows the two study sites (Wairepo Flat and South Bay).

Kaikoura

The Kaikoura peninsula is located at 42˚ 25' S, 173˚ 44' E on the north-eastern coast of the South Island of New Zealand, 200km north of Christchurch (Fig. 1.4). It has extensive platforms of several rock types including mudstone, limestone, greywacke and projects approximately 4km out from the mainland coast. It has a 2.2 m tidal range and because of the Kaikoura Canyon, is only a few kilometres from the continental shelf. It lies close to the Kaikoura Canyon and is exposed to pulses of upwelling cold water throughout the year, with annual sea-surface temperatures ranging from 9-18˚C (Chiswell & Schiel 2001). Rivers to the south of the Kaikoura peninsula can influence turbidity and sedimentation of nearshore waters. The majority of the reef platforms are algal dominated, with only patches dominated by invertebrates.

Wairepo reef (Fig. 1.5) is a mudstone platform on the North side of the Kaikoura peninsula. It is a semi-exposed reef platform facing away from the prevailing southerly swell, and is also protected by extensive outer reefs, but is unprotected from storm swells exceeding 2.5 m (Schiel & Taylor 1999). Wairepo reef is dominated by the fucoid alga

Hormosira banksii in the mid shore zone. Several species commonly inhabit the benthos below the *Hormosira banksii* canopy, including, *Corallina officinalis*, *Cystophora torulosa*, *Champia novae-zealandia*, *Colpomenia sinuosa*, *Lophothamnion hirtum* and *Carpophyllum maschalocarpum* (Fig 1.6.; Schiel & Taylor 1999; Lilley & Schiel 2006). In the lower part of the shore there is a transition zone, where *Hormosira banksii* and *Cystophora torulosa* occur in equal abundance, and below this *Cystophora torulosa* dominates. The immediate subtidal is dominated by the fucoid alga *Carpophyllum maschalocarpum*.

South Bay Reef (Fig. 1.7) is a mudstone platform on the south side of the Kaikoura peninsula. It has a south-west aspect making it moderately sheltered to prevailing southerlies, but it is much more exposed to storm waves than the northern, Wairepo Reef site. Due primarily to the rivers south of the Kaikoura peninsula, South Bay receives a higher input of sediments than Wairepo reef. Although the canopy is dominated by *Hormosira banksii*, the subcanopy is different to Wairepo reef, and is dominated by a mix of *Corallina officinalis* and ephemeral algae, such as *Polysiphonia decipiens*, and *Ulva spp*, during the warmer months.

Figure 1.5. Wairepo Reef, Kaikoura, New Zealand.

Figure 1.6. Understory algal assemblage of Wairepo Reef, Kaikoura, New Zealand.

Figure 1.7. South Bay Reef Kaikoura, New Zealand.

Moeraki

The Moeraki peninsula is located at 45˚ 11' S, 170˚ 98' E, 520km south west of Kaikoura (Fig. 1.8). It has a range of sedimentary/metamorphic platforms from mudstone to hard basaltic basement rock (Schiel & Taylor 1999). The north side of the peninsula is largely sheltered from the prevailing southerly swells, but is still subjected to high wave force. The reefs are dominated by the fucoid algae *Hormosira banksii* and *Cystophora torulosa* in the mid tide zone and *Durvillaea antarctica* in the lower tidal levels.

North Reef (Fig. 1.9) is on the northern tip of the Moeraki peninsula and faces north-east making it relatively sheltered compared to the southern facing shores of the peninsula. It is somewhat protected by outer reefs, but large swells, rarely less than 1 m in height, still reach the outer platforms (Taylor & Schiel 2005). These outer platforms are covered by *Durvillaea antarctica* at the 0-0.25m tidal level.

Figure 1.8. North Reef, Moeraki, New Zealand.

1.3.2. *The intertidal zone of north-western USA*

Oregon is at a similar latitude to southern New Zealand and the upper shore-heights are dominated by fucoid algae. However, there are several notable differences between New Zealand and Oregon systems. On the coast of Oregon a rich mosaic of algal species coexist particularly at the lower and upper tidal heights (Menge et al. 1993), with the mid-tidal range dominated by the mussel *Mytilus californianus* (Dahlhoff & Menge 1996). The fucoid alga *Fucus gardneri* is most abundant in the lower and mid-tidal zones especially on semi-protected shores and is often closely associated with barnacles. *Pelvetiopsis limitata*, an extremely hardy fucoid, is abundant in the upper tidal zone of many intertidal sites. Unlike most intertidal areas of south eastern New Zealand, the coast of Oregon has large invertebrate assemblages, predominantly comprised of the mussel *M. californianus* and balanoid barnacles, as well as large populations of the urchin, *Strongylocentrotus purpuratus* and the predatory seastar, *Pisaster ochraceus* (Connolly et al. 2001). The higher tidal zones also have large populations of the barnacles *Balanus glandula* and *Chthamalus dalli*.

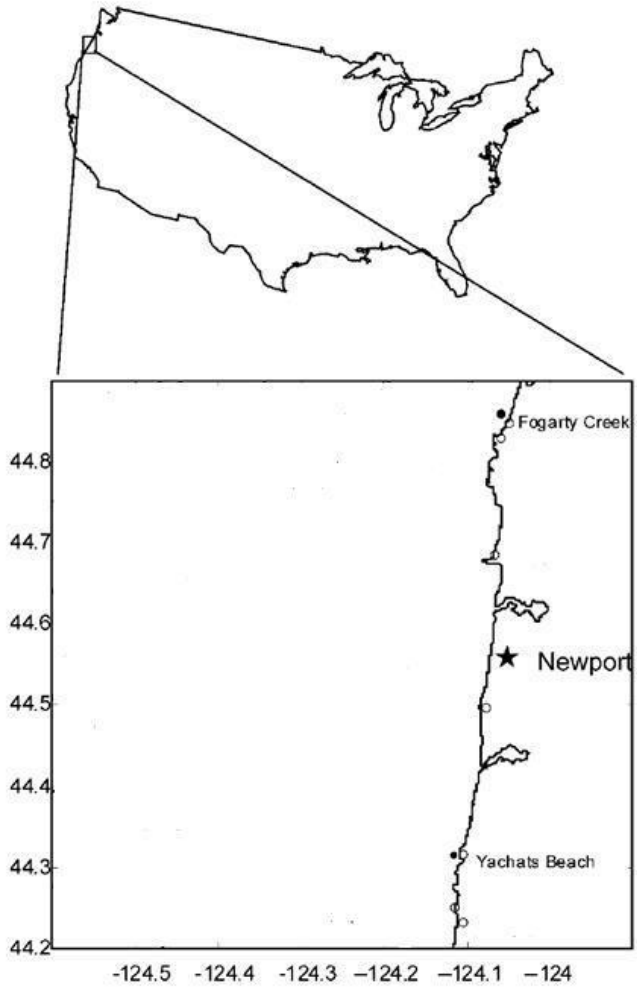

Figure 1.9. Map showing Oregon, on the west coast of the USA and the two sites Fogarty Creek, just north of Depoe Bay and Yachats Reef, just south of Waldport.

Oregon

The Fogarty Creek site is a basaltic platform located at 44˚ 51' N, 124˚ 03' W approximately 33km north of Newport (Fig. 1.9). Parts of the platform are exposed to full oceanic swells but semi-protected areas are also present (Blanchette 1996). The upper tidal levels are dominated by *Fucus gardneri*, *Pelvetiopsis limitata*, *Mastocarpus papillatus*, *Mazzaella cornocopiae*, and *Endocladia muricata* (Fig 1.10). High numbers of the barnacle *Balanus glandula* and *Chthamalus dalli* are interspersed within the macroalgal assemblages. Juvenile *Mytilus californianus* are common beneath macroalgal canopies, and adult mussels form a dense band in the mid-tidal zone, between the two algal dominated zones.

The Yachats Reef site (Fig. 1.11) is a basaltic reef intermixed with sediment-filled channels, approximately 35 km south of Newport (Fig. 1.9). Like the Fogarty Creek site, it is exposed to oceanic swells, but has some protection because of the presence of outer reefs. The upper tidal level is dominated by *Fucus gardneri*, *Pelvetiopsis limitata*, *Endocladia muricata*, *Rhodomela larix*, *Ulva* spp and *Mastocarpus papillatus*. The barnacles *Balanus glandula* and *Chthamalus dalli* are present in great abundance outside and below algal canopies.

Figure 1.10. Fogarty Creek Reef, Oregon, USA.

Figure 1.11. Yachats Reef, Oregon, USA.

California

Bodega Bay is 100 km north of San Francisco, California. The study site was 4km north-west of Bodega Bay township on the open coast along Coast Highway 1 (Fig. 1.12). On the exposed shore North of Bodega Bay (Fig. 1.13), the reef is made of basaltic boulders which protrude from an otherwise sandy beach. The higher shore boulders are dominated by *Fucus distuchus* with several species occurring below and outside the canopy, including *Corallina officinalis*, *Rhodomelia larix* and *Endocladia muricata*. The lower shore is dominated by the tough intertidal kelp *Egregia menziesii*. There are very high numbers of the barnacles *Balanus glandula* and *Chthamalus dalli* outside and below algal canopies. The mussel *Mytilus californianus* occurs in high density in the mid tidal zone.

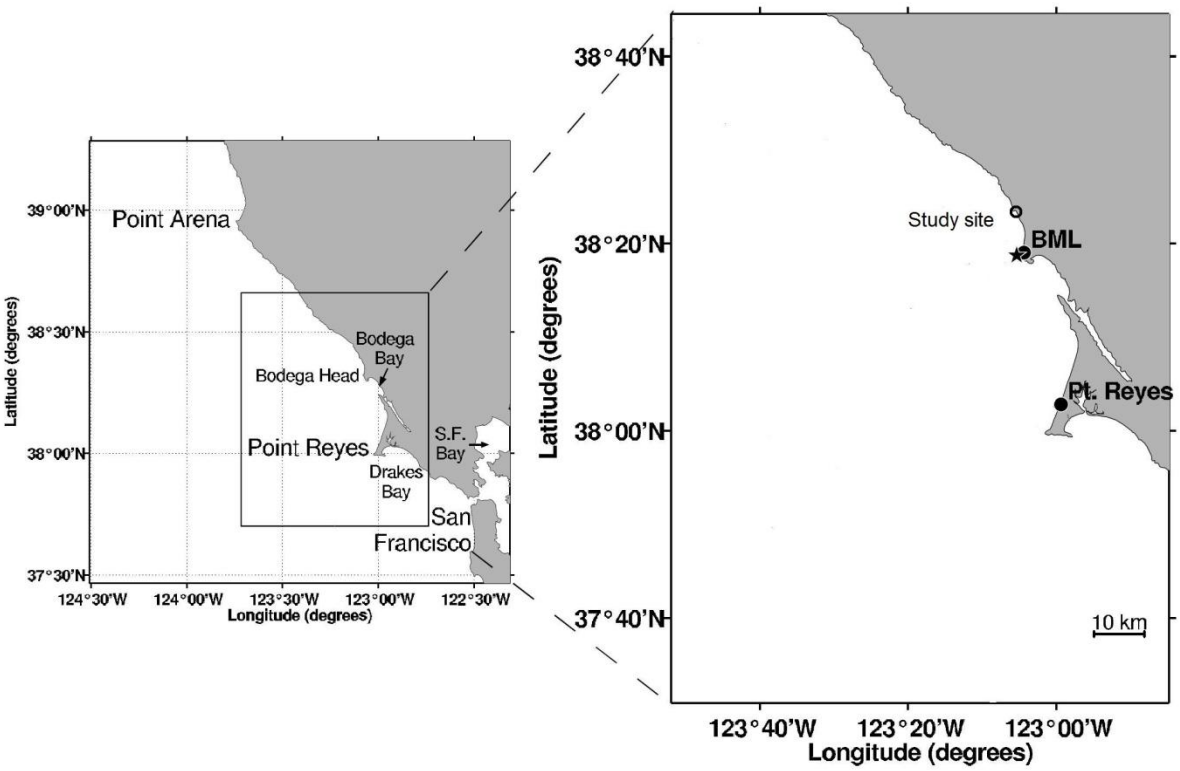

Figure 1.12. Map of California, west coast of the USA, and the study site just north of Bodega Marine Lab (BML).

Figure 1.13. Bodega Bay, California, USA.

1.4 Study species

Hormosira banksii

Hormosira banksii (Turner) Decaisne is a dioecious fucoid alga widespread throughout sheltered and moderately exposed shores of New Zealand and south-eastern Australia. It forms dense beds in the high to low littoral zone (Morton & Miller 1968) and is characterised by its brown beaded-like structure, making it unique in appearance (Adams 1994). The beaded bladders are filled with fluid providing protection from desiccation during low tide and making it well adapted to life in the intertidal zone (Bergquist 1959). It is the only large dominant perennial species that occurs widely in the mid-intertidal zone across New Zealand shores (Morton & Miller 1968; Schiel & Taylor 1999). It is polymorphic, growing in various forms across a wide range of intertidal habitats, growing up to 40cm in length (Osborn 1948; Bergquist 1959). *H. banksii* has a standing crop wet weight biomass of 7.45 $kg^{-1}m^{-2}$ at Kaikoura and 7.9 $kg^{-1}m^{-2}$ at Moeraki (Lilley 2004). Numerous algal species occupy the canopy, subcanopy and basal assemblages of the study sites. These can include well over 100 genera (Schiel, unpublished data). However, a few species were central to this thesis, and they are described here.

Cystophora torulosa

Cystophora torulosa (R. Brown) J. Agardh is a monoecious fucoid perennial alga (Adams 1994). *C. torulosa* can reach up to 1 m in length subtidally, but is typically much shorter in the intertidal zone, usually reaching sizes no greater than 30cm. It dominates the immediate subtidal on southern New Zealand wave protected shores along with two species of the same genus (*C. scalaris* and *C. retroflexa*). It forms dense canopies in the low intertidal zone, but occurs sporadically in the understory of *Hormosira banksii* canopy in the mid-high intertidal zone (Schiel 2006).

Durvillaea antarctica

Durvillaea antarctica (Chamisso) Hariot is a dioecious fucoid alga that can grow to very large sizes, with single plants occasionally exceeding 10m length and 20kg in biomass (Adams 1994). It is the largest fucoid alga, and is surpassed in size only by a few of the largest laminarian species (Hurd 2000). It has a solid cylindrical bare stipe c. 50cm long supporting a broad flattened blade, often divided into whip-like thongs. The blade has a honeycomb-like internal structure which enables it to stay buoyant (Adams 1994). It

forms large dense stands on the intertidal-subtidal margin and is a conspicuous component of exposed reefs throughout southern New Zealand. In New Zealand it is regularly found above *Durvillaea willana*, which is strictly subtidal.

Corallina officinalis

Corallina officinalis Linnaeus is a red, geniculate, coralline algal species. *C. officinalis* stands at about 4cm high, and is found on wave-protected and moderately exposed shores around New Zealand (Adams 1994). It is made up of calcified segments alternating with uncalcified joints (Adams 1994). The highly branched and dense structure of *C. officinalis* often leads to a large build-up of silt and sand (Morton & Miller 1968). At the base of the turf is a cover of dull pink encrusting coralline algae. This is the basal form of *C. officinalis* which first appears in recolonisation (Schiel & Taylor 1999; Lilley & Schiel 2006; Schiel & Lilley 2007).

Figure 1.14. New Zealand macroalgal species. Top left *Hormosira banksii*, top right, *Cystophora torulosa* next to the thicker bladed *Xiphophora gladiata*, bottom left *Corallina officinalis*, and bottom right *Durvillaea antarctica*.

Fucus gardneri

Fucus gardneri (L.) Powell is monoecious fucoid alga in the upper and mid intertidal throughout North America from Alaska to California (Abbott & Hollenberg 1976). Its thalli grow from a discoid holdfast with dichotomous branching. It has gas-filled pneumatocysts, most likely aiding in desiccation resistance. It ranges in size from 10-25cm length depending upon exposure, but rarely exceeds 25cm (Blanchette 1997; Abbott & Hollenberg 1976). It provides habitat for several invertebrate grazer species including the snails *Tegula funebralis*, *Littorina scutulata* and several species of limpets.

Pelvetiopsis limitata

Pelvetiopsis limitata (Setchell) Gardner has thalli 4-8cm tall with erect flat branches. It is found in the upper intertidal zone and occurs from Vancouver island to central California (Abbott & Hollenberg 1976). *Pelvetiopsis limitata* is a monoecious fucoid alga, it is smaller than *Fucus gardneri*, and has narrower branches. It often dominates the high intertidal zone, but is also found lower in the shore, often amongst *Fucus gardneri*.

Mazzaella cornocopiae

Mazzaella cornocopiae (Postels & Ruprecht), is a red alga that occurs in clumps in the mid to upper intertidal zone (Abbott & Hollenberg 1976). It has short stipes, flaring into furrowed apophyses, and divided once or twice into narrow lobes. It is usually 2-4cm long and occurs in very tight clumps often with *Mastocarpus papillatus*. *Mazzaella cornocopiae* is found from Alaska to California and is also found in Japan (Abbott & Hollenberg 1976).

Figure 1.15. Oregon macroalgal species, top *Fucus distichus* at Yachats reef and at Fogarty Creek reef (inset), middle *Pelvetiopsis limitata* (yellow brown) surrounding *Mastocarpus papillatus* (red), and bottom *Mazzaella cornocopiae* forming a dense turf and single thalli (inset; Photos by: David Schiel).

Primary production dynamics

Role of community composition in the production of natural macroalgal assemblages

2.1. Introduction

Understanding the quantity of biomass output from primary production is essential in estimating energy budgets of ecosystems. Furthermore, a baseline estimate of primary production is essential for identifying future changes in biomass export. Although estimations of phytoplankton production are relatively well advanced (Falkowski et al. 1998), large-scale primary production of macroalgae has received little attention (Mann 1973; Miller et al. 2009; Cavanaugh et al. 2010). Several studies have defined photosynthetic characteristics of macroalgae (Littler & Littler 1980; Littler & Arnold 1982), but many of these have failed to scale up primary production to ecosystems or communities. Furthermore, attempts to estimate large-scale annual primary production of macroalgae have typically focused on the giant kelp *Macrocystis pyrifera* or other common laminarians (Mann 1973; Jackson 1977; Reed et al. 2008). Even within the same genus or species, estimates of annual production differ significantly between researchers (i.e., annual production of *M. pyrifera* estimated between 537 and 2380 g C m^{-2} yr^{-1} depending upon study, Jackson 1977; Reed et al. 2008). The discrepancy in results is possibly due to the variety of techniques used to measure production, the way these methods are implemented and the duration of the study. Therefore, a greater understanding of primary production dynamics may help us better understand the contribution of macroalgae to marine food webs.

Primary production of macroalgae can be measured in a number of ways: biomass accumulation, photorespirometry, and pulse amplitude modulated (PAM) fluorometry. Primary production of large macrophytes has typically been measured using frond growth increment techniques (Mann 1973). These methods are useful for estimating *in situ* growth rates of large kelps such as *M. pyrifera* which are difficult to examine under laboratory conditions (Reed et al. 2008). Furthermore, *in situ* measurements give a natural representation of growth rates, seasonal differences and site differences (Mann 1973; Reed et al. 2008). Estimations of annual primary production in *M. pyrifera*, probably the most studied of all rocky-shore marine macroalgae, vary significantly depending upon the author. Research by Mann (1973) predicts an annual production of 1750 g C m^{-2} yr^{-1}, whereas more recent research (Reed et al. 2008) estimates an annual production of up to 2300 g dry mass m^{-2} yr^{-1}. Although the differences may represent scientific advancement since Mann's 1973 study, it still indicates a large variation in results within the same species. Furthermore, when primary production is estimated using different techniques,

such as photorespirometry, the results are different again. Jackson (1977), used photorespirometry, coupled with a range of environmental variables to estimate annual growth of *M. pyrifera*, giving a net production of 537 g $Cm^{-2}yr^{-1}$, significantly lower than estimates from Mann (1973) and Reed et al. (2008). Understanding which methods and results are most relevant to actual primary production rates of macroalgae is essential to furthering our understanding of these important autotrophic assemblages.

Although useful for identifying seasonal biomass accumulation, *in situ* measurements of frond elongation fail to factor in processes such as abrasion, herbivory, reproduction and sloughing into estimations of primary production (Larkum 1986; Murthey et al. 1986). Likewise, photorespirometry measurements have potential problems. In particular, they are typically done using single thalli or excised tissue sections (e.g., Littler & Littler 1980; Littler & Arnold 1982), although the use of *in situ* photorespirometry by Miller et al (2009) is a notable exception. PAM fluorometry provides an *in situ* test of primary production, but is often hard to extrapolate to a change in biomass or a value of carbon fixation (Beer & Axelsson 2004). Measuring photosynthesis using PAM fluorometry gives production as electron transport rate (the effective quantum yield of photosystem II), which is difficult to convert into an estimate of carbon fixation (Beer & Axelsson 2004). Some studies have attempted to couple PAM measurements with photorespirometry measurements of oxygen evolution to quantify primary production using PAM (Franklin & Badger 2001; Beer & Axelsson 2003; Schwarz et al. 2003; Schwarz et al. 2005). Another problem associated with PAM fluorometry is its use of chlorophyll A as an indicator of primary production, with many marine macroalgal species containing a range of photosynthetic pigments (Gröniger et al. 2000). To gain a realistic estimation of primary production, the use of photorespirometry using whole communities may provide an important counterpoint to other primary production research.

Macroalgae generally occur in diverse stands, composed of several species, often found at several canopy layers (Reed & Foster 1984; Lilley & Schiel 2006; Schiel & Lilley 2007). The effects of assemblage composition on primary production may help form a model of annual production at an ecosystem scale. Research has indicated the importance of algal density and diversity on the utilisation of light (Binzer & Sand-Jensen 2002a; Middelboe & Binzer 2004) and reveals the problems associated with measuring production in single specimens (or excised tissue). Light absorption at different canopy layers may result in greater utilisation of light, and therefore, a more linear relationship

between production and irradiance (as opposed to saturation curve seen in single species incubations; Binzer & Sand-Jensen 2002a). Assemblage-based incubations also show a lack of photoinhibition at high irradiance, as is typically seen in single species incubations (Middelboe & Binzer 2004). Understanding how assemblages, compared to their components, use light may help elucidate the dynamics of primary production in real communities. To obtain realistic estimates of primary production in natural ecosystems the resource partitioning of multi-species assemblages must be considered.

In order to understand the dynamics of photosynthesis and production within macroalgae, I used a variety of techniques: photorespiration of single thalli, entire communities and *in situ* PAM fluorometry. Comparisons among these techniques enabled me to determine the most accurate and effective method of measuring photosynthesis within macroalgae. Examining single thalli and assemblages will help our understanding of how the production of a community compares to the sum of its parts and if important interactions are occurring between co-existing species. Here I used natural macroalgal assemblages taken from the field and tested under controlled laboratory conditions to evaluate primary production and light use efficiency using measurements of net photosynthesis or oxygen evolution (as a proxy for carbon fixation during primary production). I tested the null hypothesis that canopy and assemblage structure have no effect on net photosynthesis in algal assemblages.

2.2. Methods

2.2.1. *Study sites*

Macroalgae were collected from various sites on the Kaikoura Peninsula on the east coast of New Zealand's south island. Single thalli were removed from the substrate using a knife under the holdfast and bought back to the laboratory. Single thalli experiments were done between December 2007 and June 2008. Macroalgal assemblages were removed by cutting moderate sized sections of the substrate, along with the attached algae. This was done using a chisel and hammer to break sections of rock from the reef. *In situ* PAM fluorometry was done on Wairepo Reef on the northern side of Kaikoura Peninsula on mid to high tide during winter and spring 2009 (July-September).

2.2.2. *Production of individual thalli*

Instantaneous primary production of individual specimens (single thallus) was measured by incubating algae under a range of irradiances and measuring net increases in oxygen. Several species of algae were incubated in perspex chambers under a range of irradiances. Temperature was controlled using a water jacket that surrounded the chamber. Water within the jacket was pumped from a temperature-controlled water bath to the chamber using a submerged magnetic water pump. Chambers were kept at a constant 15˚C, which was verified using internal temperature loggers. Chambers used for single thallus incubations were 15cm in diametre and 15cm high to accommodate an entire algal thallus (Fig. 2.1). To prevent boundary layers forming on the algal surface (which could potentially limit photosynthesis), chambers were constantly mixed using a magnetic flea. Water samples were extracted with 1mL syringes and oxygen concentration was measured in a Clark-type oxygen electrode (StrathKelvin). Oxygen production was converted into carbon fixation using a photosynthetic quotient of 1.1, as used in other studies on temperate algae (Littler & Arnold 1982; Hanelt et al. 2003). Samples were taken half-hourly for production and respiration measurements over an hour for each irradiance level, with an incubation series on each assemblage lasting approximately 7 hours.

Algae were incubated under various light intensities using a Phillips Discharge metal halide lamp calibrated to PAR (Photosynthetic Active Radiation) wavelengths, with irradiance adjusted using neutral density filters to give five levels of irradiance (150, 300, 800, 1500 and 2000 μmol m^{-2} s^{-1}). Dark respiration was obtained by covering the chamber to omit light. Measurements of dark respiration were performed at least one hour after algae had been exposed to light to minimise the inclusion of photorespiration in the results. Measurements of respiration were only used to obtain baseline respiration rates and were not incorporated into values for net photosynthesis. In total, 6 replicates of each assemblage component were incubated under all levels of irradiance. Following incubations, algae were dried for 24 hours in a conventional oven at 50 ˚C and dry weights recorded.

The species examined included four commonly-occurring, habitat dominant fucoid algae. The fucoid algae tested were found at various shore heights from mid intertidal to immediate sub-tidal. The four species occurring highest to lowest were *Hormosira banksii*, *Cystophora torulosa*, *Durvillaea antarctica*, and *Carpophyllum*

maschalocarpum. *H. banksii*, *C. torulosa*, and *C. maschalocarpum* were all dominant on sheltered shores, whereas *D. antarctica* is common on exposed shores. Two ephemeral species *Ulva spp*, and *Porphyra spp*, one invasive laminarian species *Undaria pinnatifida* and the ubiquitous calcareous turf forming assemblage, dominated by *Corallina officinalis* (referred to as basal assemblage) were also examined to allow comparisons with other growth forms of macroalgae. Examining a single thallus of *C. officinalis* was difficult due to its very small size. Furthermore, this species forms a dense turf and often has a range of algal species living in and on it. For these reasons it was tested as a turfing assemblage.

To validate laboratory-based incubations with naturally occurring assemblages, PAM fluorometry was used on macroalgal specimens *in situ*. A diving PAM fluorometer (Heinz Walz GmbH©) was used to analyse macroalgal specimens. PAM fluorometry was done on attached macroalgae *in situ*, using natural variation in irradiance during different light conditions. Natural photosynthetic active radiation (PAR) was measured using the light sensor attachment of the PAM fluorometer. The end of the fibre-optic cable was placed at a standard 1cm away from the algal surface for all measurements, and was always submerged, with care taken to orientate the light sensor correctly (i.e., facing upwards and not shaded by the user). Electron transport rate (ETR) calculated by the fluorometer was used for analysis of data. For analysis, primary production at given levels of natural irradiance were grouped into 7 ranges of irradiance, being 0-50, 51-400, 401-600, 601-1000, 1001-1400, 1401-1800, and 1801+. Fluorometry was done on three of the most common intertidal algae on sheltered shores, *H. banksii*, *C. torulosa*, and *C. officinalis*.

2.2.3. *Macroalgal assemblage primary production*

To test the importance of structure in natural assemblages, primary production was tested in intact macroalgal assemblages. Using a hammer and chisel, macroalgal assemblages were removed from the reef with substrata attached (approximately 20x20cm of substratum). These were taken back to the lab where all incubations were done. The methodology used above for single species production was also used for the macroalgal assemblages. To accommodate the macroalgal assemblages, large incubation chambers were used (Fig. 2.2). These were made of a clear Perspex tube (30 cm high, 25cm diameter and 8mm thick), with a 10mm thick clear perspex base plate and lid (Tait & Schiel, in press). Unlike the chambers used for single species incubations, these chambers

did not have a cooling water jacket, so temperature was controlled by placing chambers in a constant temperature water bath and maintained at 15˚C, which was verified using internal temperature loggers (Fig. 2.3). The same light source used in the single thallus incubations was used for macroalgal assemblages. Chambers were mixed using a submerged magnetic water pump that circulated water within the chamber in a vortex motion. Water samples were taken from taps in the lid of the chamber. Completely intact macroalgal assemblages were incubated under the same irradiance regime as for single species. All visible invertebrates were removed from the community before incubations. The volume displaced by the substratum was accounted for after all incubations to determine the oxygen evolved per litre of water. Oxygen production was converted into carbon fixation using a photosynthetic quotient of 1.1, as used in other studies on temperate algae (Littler & Arnold 1982; Hanelt et al. 2003).

To understand primary production dynamics in macroalgal assemblages, four types of assemblages were analysed. These assemblages were dominated by *H. banksii*, *C. torulosa*, *D. antarctica* and *Porphyra spp* and included a range of less dominant subcanopy species. As in single thallus incubations, these species were subjected to five levels of irradiance 150, 300, 800, 1500 and 2000 μmol m^{-2} s^{-1}. Also, dark respiration was measured by covering chambers with a dark cloth to omit light. Productivity vs. irradiance (P-E) curves were generated for these assemblages (n = 6) and compared to the production of the dominant species incubated alone (using data from single thallus incubations, *see above*). Production of assemblages vs. production of the dominant species incubated alone was done per gram weight of algal tissue and averaged across 5 levels of irradiance 150, 300, 800, 1500 and 2000 μmol m^{-2} s^{-1}. This allowed for estimation of the contribution of the dominant species compared to the entire assemblage.

2.2.4. *Effects of canopy removal on primary production dynamics*

To test the comparative roles of canopy and subcanopy species on primary production, a series of removal experiments were done on assemblages dominated by *H. banksii*. First, intact assemblages removed from the field were incubated in the laboratory using the same experimental procedure used in other laboratory incubations. After intact assemblage incubations were completed, the dominant canopy and subcanopy species were sequentially removed from the assemblage and oxygen production measured. The effect of species loss was tested by removing one or both of the dominant fucoid algae, *C.*

torulosa and *H. banksii*. The order of removal was changed to determine the role of each species within the assemblage. Also, the role of the subcanopy was tested by first removing the basal assemblage (dominated by *C. officinalis* and various epiphytes) then *C. torulosa* the other dominant subcanopy species. This left only *H. banksii* (the dominant canopy species) in the final incubation series. At all combinations in all treatments, 8 replicate assemblages were tested. The loss of macroalgal biomass was taken into account by standardising all data for the remaining biomass of macroalgae.

To analyse differences between treatments several standard photosynthetic parameters were calculated. The parameters used were α, γ (instead of β, which is typically used in saturating curves), R, E_c, and P_{2000}, (the net photosynthesis at 2000 μmol m^{-2} s^{-1}). Due to the lack of saturation in photosynthesis a *Pm* could not be calculated for all assemblages, therefore, a value of P was restricted to the highest level of irradiance tested (i.e., P_{2000} at 2000 μmol m^{-2} s^{-1}). Furthermore, photoinhibition or β was not observed in all assemblages and was, therefore, changed to γ, and was not a factor testing photoinhibition, but the direction of change from 1500-2000 μmol m^{-2} s^{-1}. Therefore, γ can represent a positive (increase in production) or negative (photoinhibition) of assemblages. Also, E_c the irradiance at compensation (γ = 0) for all assemblages was calculated, but due to the lack of saturation in assemblages E_k was not calculated. The differences in these photosynthetic parameters between assemblages were examined using one-way ANOVA and Tukey's post-hoc tests.

To compare the primary production of algae incubated alone with intact assemblages, an additive value was derived from the production of the three assemblage components (*H. banksii*, *C. torulosa* and basal assemblage). Although the basal assemblage was composed of several species, these were found in very low amounts and differed significantly between replicates. Therefore, all the low-lying species were grouped together as the basal assemblage for analysis. Values were calculated at 5 levels of irradiance (150, 300, 800, 1500 and 2000 μmol m^{-2} s^{-1}) by first weighting the production of each component by its average contribution to the assemblage (on a dry weight basis), then adding the three production values together. The average contribution of each species to the assemblage was determined by the relative species weights in the incubations of intact communities. This allowed comparisons to determine if an assemblage acts as the sum of its parts, or if species interactions within naturally occurring assemblages have a significant effect on overall primary production.

The role of layering and assemblage structure was further analysed by removing the algal specimens from the substratum. Assemblage structure was disassembled to gain an understanding of the role that canopy layers have in overall primary production. Macroalgae was removed from the field using a template 25cm in diameter (same diameter as the incubation chamber) and then incubated in the lab using the same techniques as mentioned above (for assemblage production). Algae was placed in the chamber (n = 6) with no regard for assemblage structure and allowed to free float. The production at four levels of irradiance (150, 800, 1500 and 2000 μmol m^{-2} s^{-1}) was then compared to the production of an intact assemblage at the same irradiance levels (n = 6).

2.2.5. *Algal diversity and primary production*

The influence of biodiversity on overall primary production was tested using the natural variation of diversity within the assemblages (for assemblages dominated by *H. banksii* only). All visible macroalgal species within the assemblages were identified and counted prior to incubations. Also, experiments in which species had been removed were also included in the analysis of the impact of species diversity on production. The total number of species in the incubations, experimental or control was used to analyse the role of algal diversity on primary production. Therefore, this analysis includes both natural variation in species diversity as well as the effects of non-random species removal (from above canopy and subcanopy removal experiments).

The influence of canopy structure on overall primary production was tested using data from previous removal experiments (described above). Canopy, subcanopy and basal assemblage removal experiments were used to determine the role of canopy layers on production at various irradiance levels. All assemblages, manipulated and intact, were categorised into three types: three assemblage layers or intact (i.e., *H. banksii*, *C. torulosa* and basal assemblage), two assemblage layers (two of the three assemblage layers), and one assemblage layer (only one of the three assemblage layers). All production data were standardised by the dry weight of algae within the assemblages. The effects of canopy complexity on production were analysed at three levels of irradiance, 800, 1500 and 2000 μmol m^{-2} s^{-1}.

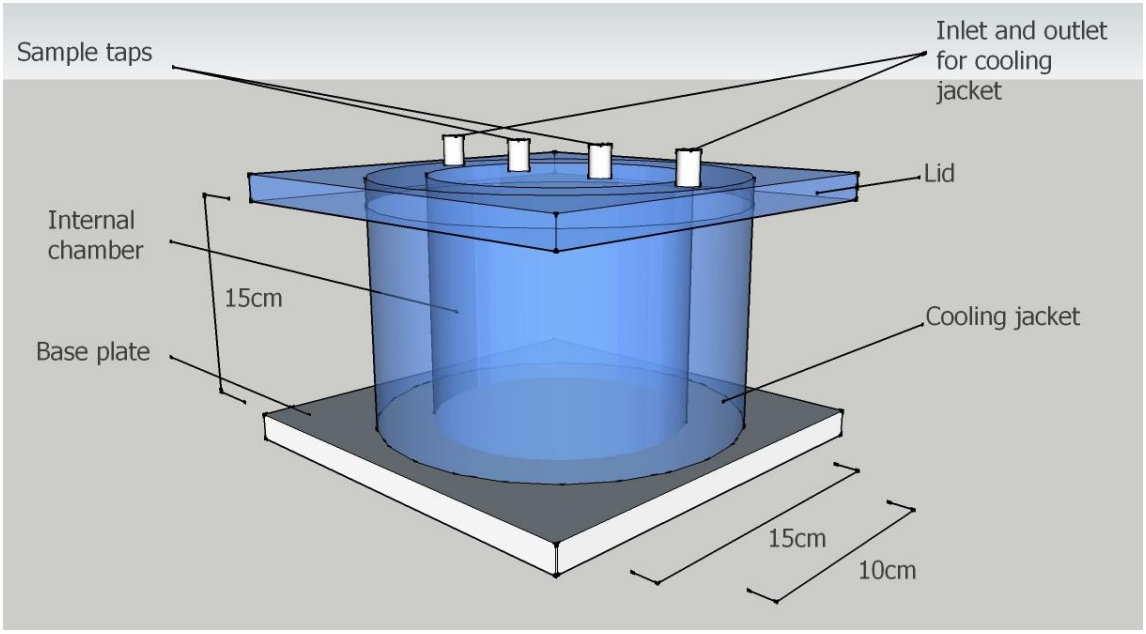

Figure 2.1. Design and dimensions of incubation chamber for single thalli.

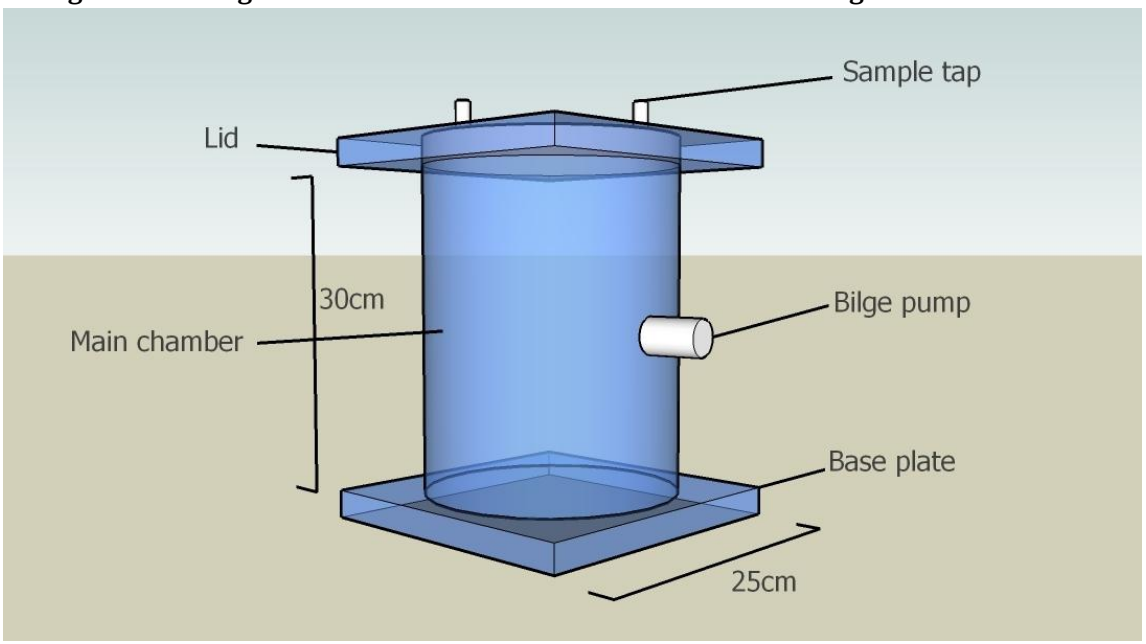

Figure 2.2. Design and dimensions of laboratory incubation chamber for macroalgal assemblages.

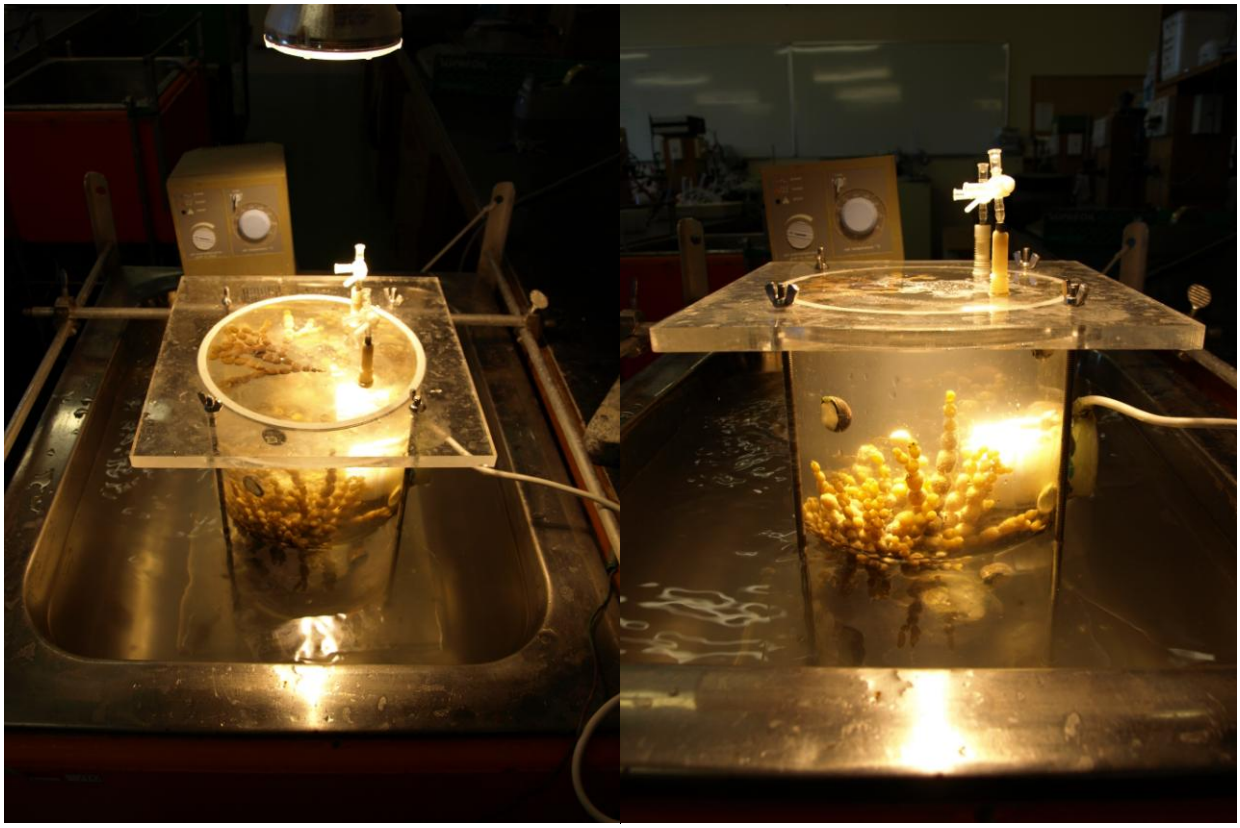

Figure 2.3. Photos showing the laboratory setup with chambers in a temperature controlled water bath, with a vertical light source. Chambers show the two taps on the lid and the bilge pump on the side used to stir the chambers.

2.3. Results

2.3.1. *Single thalli primary production*

Primary production of the four fucoid species indicated typical P-E curves with a fast initial rise, followed by saturation of production (Fig. 2.4). All curves were fitted using a rectangular hyperbola with r^2 values of *H. banksii* = 0.67, *C. torulosa* = 0.76, *D. antarctica* = 0.63, and *C. maschalocarpum* = 0.85. The level of irradiance at which saturation of photosynthesis occurred (E_k) differed between the species, with the mid-shore *H. banksii* and *C. torulosa* showing saturation at high irradiance and the low-shore *D. antarctica* and *C. maschalocarpum* showing saturation at low irradiance. One-way ANOVA indicated a significant difference in E_k between species ($F_{3,28} = 8.0$, $p < 0.0005$). Furthermore, Tukey's post-hoc tests revealed significant differences between *C. torulosa* and *D. antarctica* ($q = 5.9$, $p < 0.01$), as well as *C. torulosa* and *C. maschalocarpum* ($q =$

6.1, $p < 0.01$). The maximum production (P_{max}) of these species had a similar relationship, with a gradient from low-shore to high-shore (Fig. 2.5). The low-shore *C. maschalocarpum* had the highest P_{max} of 1.29 $mgDW^{-1}\ h^{-1}$, followed by *D. antarctica* 1.04 $mgDW^{-1}\ h^{-1}$, *C. torulosa* 83.0 $mgDW^{-1}\ h^{-1}$ and the highest living species *H. banksii* 0.44 $mgDW^{-1}\ h^{-1}$. One-way ANOVA indicates a significant difference in P_{max} between species ($F_{3,28} = 13.9$, $p < 0.0001$), and Tukey's post-hoc tests showed significant differences between *H. banksii* and *D. antarctica* ($q = 6.7$, $p < 0.001$), as well as *H. banksii* and *C. maschalocarpum* ($q = 8.4$, $p < 0.001$).

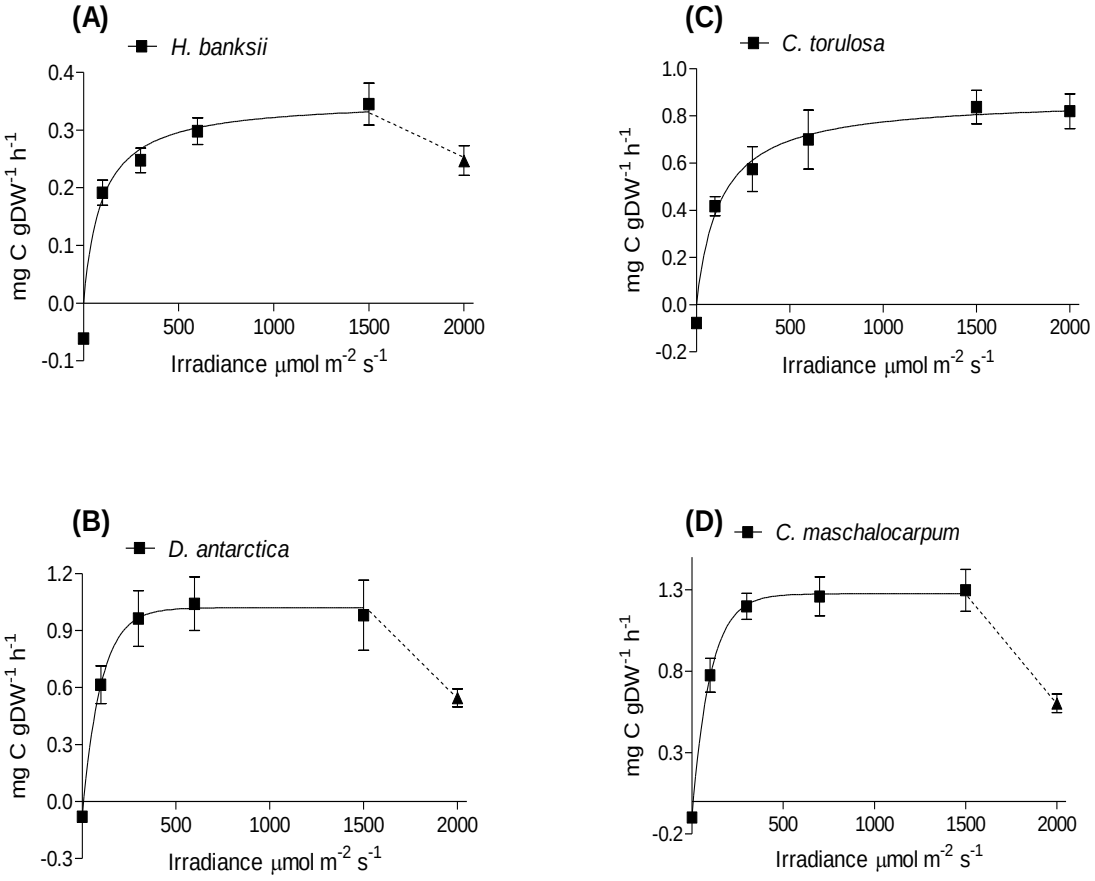

Figure 2.4. Primary production of single thalli vs. irradiance for single thalli of four common fucoid species (A) *H. banksii*, (B) *C. torulosa*, (C) *D. antarctica* and (D) *C. maschalocarpum*.

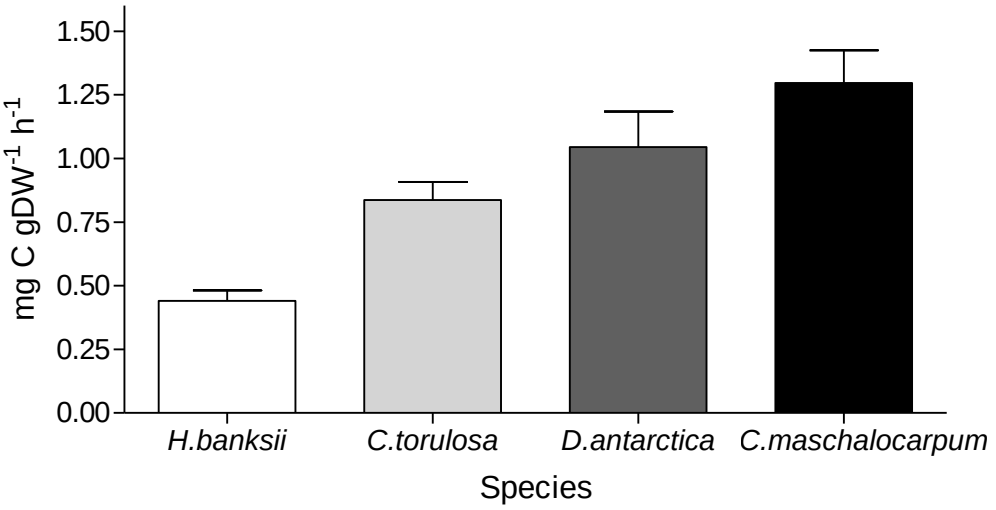

Figure 2.5. Maximum production of four common fucoid algae. Species are arranged from high-shore species (*H. banksii*) to low-shore species (*C. maschalocarpum*).

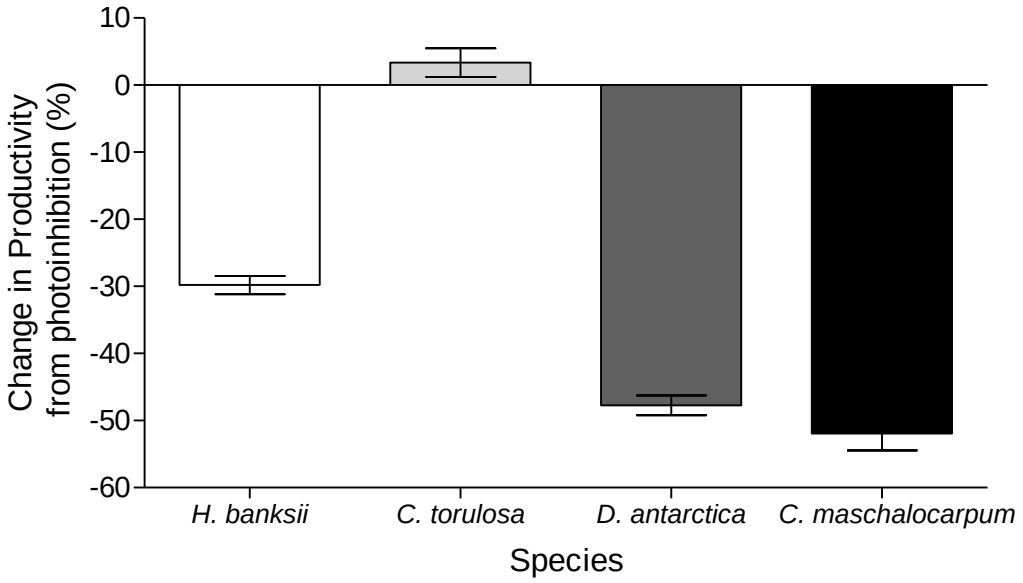

Figure 2.6. Percentage change in production caused by very high levels of irradiance (2000µmol m^{-2} s^{-1}) compared with production at 1500 µmol m^{-2} s^{-1}.

Three of the four species showed photoinhibition at the highest level of irradiance with *C. torulosa* being the only exception to this. The relative extent of the photoinhibition, like the maximum production, varied with the shore height at which the species occured, with the low-shore species showing the largest fall in production at high irradiance (Fig. 2.6). The only exception being *C. torulosa* which had no fall in primary production at high irradiance.

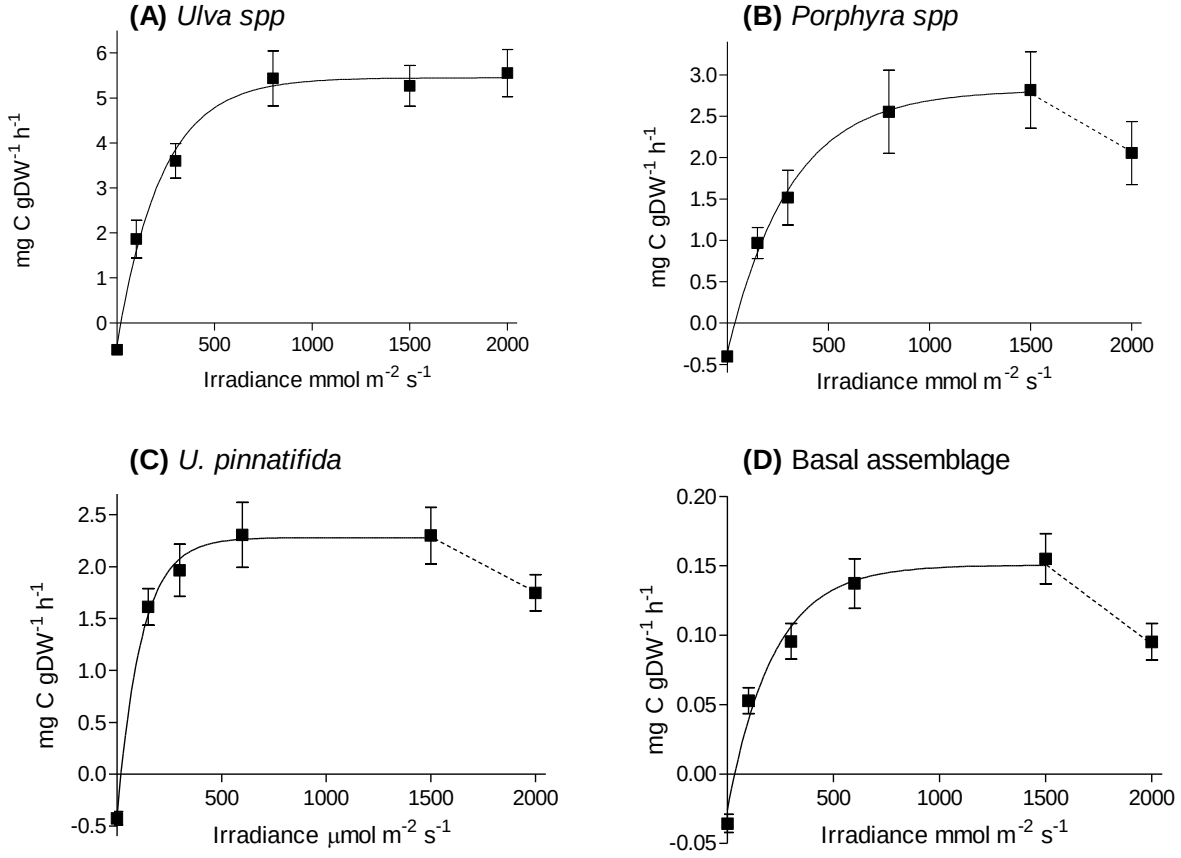

Figure 2.7. Primary production versus irradiance for four algal species. Species shown are (A) *Ulva spp.*, (B) *Porphyra spp*. (high-shore species), (C) *Undaria pinnatifida* (sub-tidal invasive species) and (D) the basal assemblage dominated by *C. officinalis*.

P-E curves for the two ephemeral species *Ulva spp* and *Porphyra spp*, the invasive laminarian *U. pinnatifida* and the turf forming *Corallina officinalis* had much the same relationship as the fucoid species (Fig. 2.7). However, the levels of primary production reached by *Ulva spp*, *Porphyra spp* and *U. pinnatifida* were much higher than those of the fucoid species, whereas the basal assemblage was the least productive species tested. The high-shore *Ulva spp* and *Porphyra spp* indicate saturation of primary production at relatively high irradiance, whereas the mainly subtidal *U. pinnatifida* showed saturation at much lower irradiance. Of the four species, *Ulva spp* had the highest P_{max} of 5.56 mg C

$gDW^{-1}h^{-1}$, followed by *Porphyra spp* 2.81 mg C $gDW^{-1}h^{-1}$, *U. pinnatifida* 2.3 mg C $gDW^{-1}h^{-1}$ and the basal assemblage 0.18 mg C $gDW^{-1}h^{-1}$ (Fig. 2.8). One-way ANOVA showed significant differences in P_{max} between species ($F_{3,28}$ = 38.7, p < 0.0001). Furthermore, Tukey's post-hoc tests indicated significant differences between all species combinations (q > 6.8, P < 0.001), except *U. pinnatifida* and *Porphyra spp*.

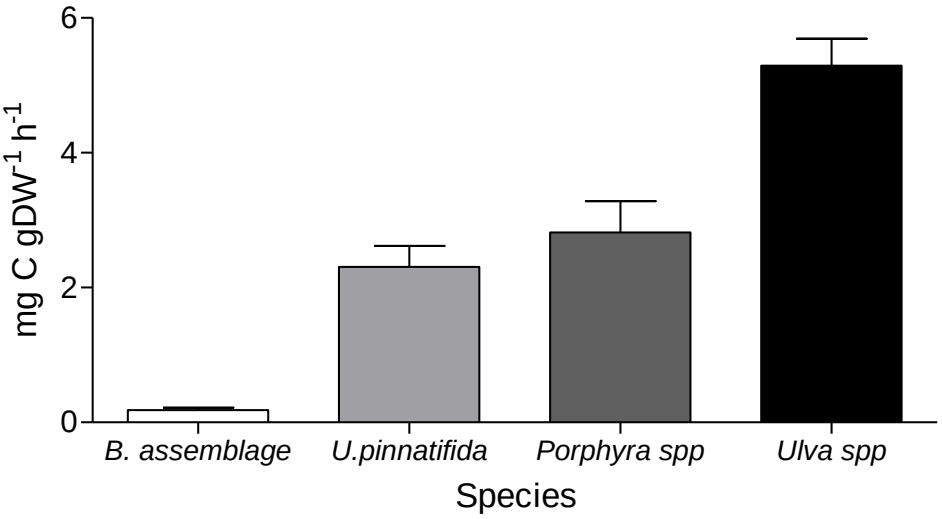

Figure 2.8. Maximum primary production of two ephemeral (*Porphyra spp.* and *Ulva spp.*), an invasive species (*U. pinnatifida*) and the basal assemblage (dominated by *C. officinalis*).

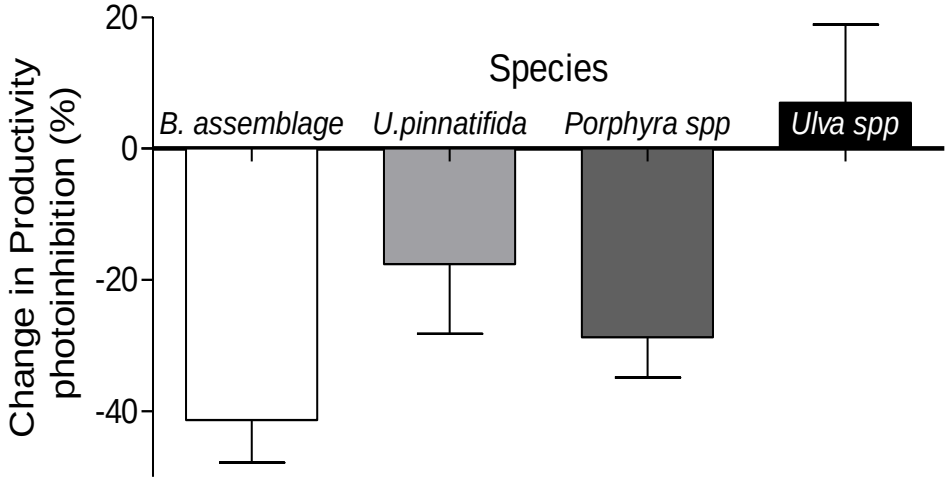

Figure 2.9. Percentage change in production caused by very high levels of irradiance (2000µmol m^{-2} s^{-1}) compared to production at 1500 µmol m^{-2} s^{-1}.

Table 2.1. Compensation points (irradiance level where net primary production is zero) for single thalli of various macroalgal species.

Species	Compensation point µmol m^{-2} s^{-1}(±SE)
Hormosira banksii	22.2 (3.8)
Cystophora torulosa	15 (2.1)
Durvillaea antarctica	10.1 (3.0)
Carpophyllum maschalocarpum	9.5 (2.4)
Basal assemblage	37.5 (4.0)
Undaria pinnatifida	21.1 (2.2)
Porphyra spp.	41.1 (4.2)
Ulva spp.	22.8 (3.8)

Compensation points of the four fucoid species *H. banksii*, *C. torulosa*, *D. antarctica*, and *C. maschalocarpum* were similar to the maximum production results, with the high-shore species having the compensation points at higher irradiance and the low-shore species at lower irradiance (Table 2.1). The high-shore species (Basal assemblage, *Ulva spp.* and *Porphyra spp.*) had compensation points at irradiance levels above 20 µmol m^{-2} s^{-1}, whereas the low-shore *U. pinnatifida* had a compensation point at lower irradiance, similar to the pattern seen in fucoid species. Furthermore, photoinhibition was seen at the highest level of irradiance in three species, *Porphyra spp.*, *U. pinnatifida*, and the basal assemblage, but not in *Ulva spp.* (Fig. 2.9), as was observed in the fucoid species.

PAM fluorometry indicated similar P-E curves to those observed in photorespirometry incubations, with typical saturation curves, and photoinhibition in both *H. banksii* and the basal assemblage (Fig. 2.10). Furthermore, as with the photorespirometry incubations, *C. torulosa* showed no sign of photoinhibition at high irradiance. Also, the relative Electron Transport Rate (ETR) of each of these species was in order with the photorespirometry incubations, with *C. torulosa* being the most productive, followed by *H. banksii* and the basal assemblage being the least productive.

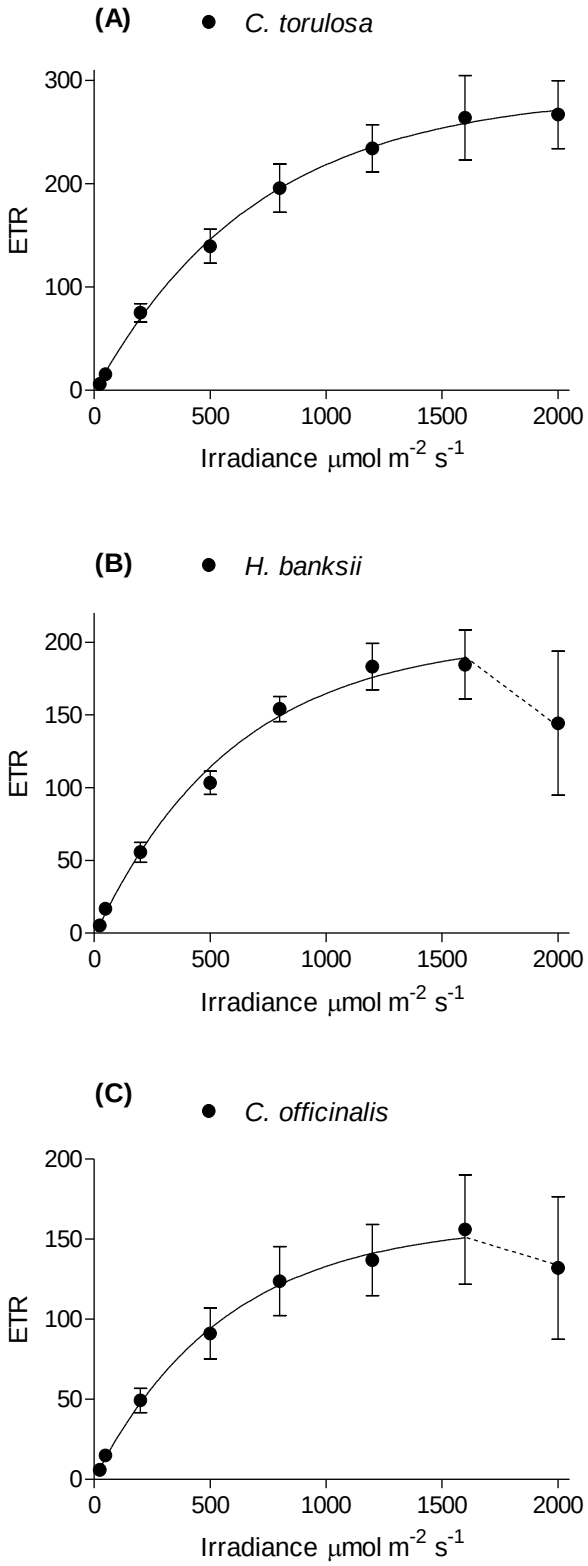

Figure 2.10. PAM fluorometry of three macroalgal species, two fucoid alga *C. torulosa* (A), *H. banksii* (B) and one calcareous turf *C. officinalis* (C). Electron Transport Rate (ETR) versus natural levels of irradiance in the field.

2.3.2. *Macroalgal assemblage primary production*

The production irradiance curves for the three fucoid assemblages all had a different relationship to that observed in single thalli incubations. *H. banksii*, *C. torulosa* and *D. antarctica* assemblages all showed no sign of saturation of photosynthesis, but had a linear increase in primary production after the initial rise in production at low light levels. The *Porphyra spp* assemblage did not show this relationship, but exhibited a typical saturation and photoinhibition curve (Fig. 2.11). Average assemblage biomass had no obvious association with per area primary production in this example (Table 2.2 & Fig. 2.11). The most productive species, *Porphyra spp*, had the lowest average biomass. One-way ANOVA and Tukey's post-hoc tests indicate that the P_{max} of *Porphyra spp* was significantly higher than that of *H. banksii* ($q = 7.2$, $p < 0.001$) and *C. torulosa* ($q = 4.0$, $p < 0.05$). Furthermore, although *C. torulosa* had the highest average biomass, it was less productive than *D. antarctica*. This was not necessarily the case in natural assemblages, but due to the size limitation of chambers only small *D. antarctica* plants could be used. The three fucoid assemblages, did show a relationship between shore height and maximum production.

When the average production of the assemblages were compared to the average production of the dominant species incubated alone, the data indicated that the assemblages were generally more productive than the main component, when standardised by dry weight of the entire assemblage (Fig. 2.12). *H. banksii* and *D. antarctica* assemblages had significantly higher average production than single thalli (Two-tailed T-test, $p < 0.05$ for both, $t = 2.06$ and $t = 2.21$ respectively), although there was no significant difference in the case of *C. torulosa*, the assemblage was more productive than the single thalli. The *Porphyra spp* assemblage was, on average, the only assemblage that did not show this trend, with higher production per thallus than in the assemblage ($t = 2.76$, $p < 0.05$).

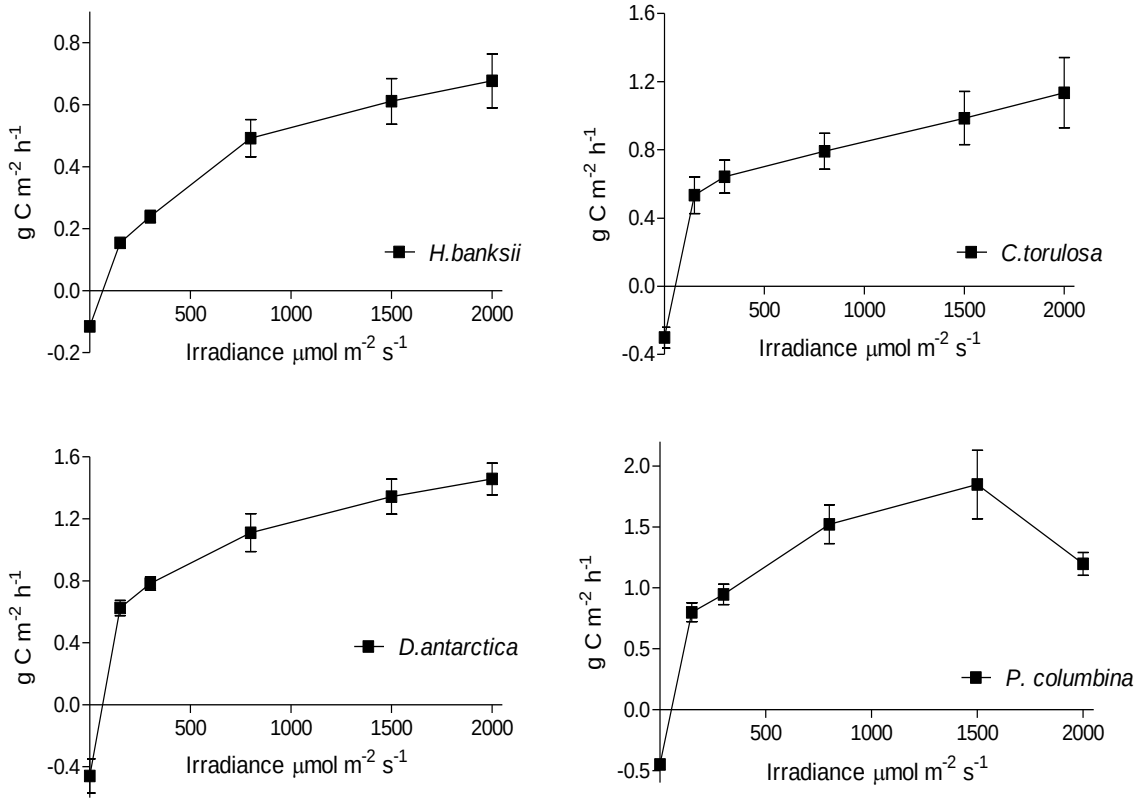

Figure 2.11. Primary production (±SE) vs. irradiance of entire algal assemblages dominated by *H. banksii*, *C. torulosa*, *D. antarctica*, and *Porphyra spp*.

Table 2.2. Average biomass (±SE) of algal material in various macroalgal assemblages and average algal diversity.

Species	Wet biomass g (±SE)	Dry biomass g (±SE)	Average species richness
Hormosira banksii	359.8 (73)	71.96 (14)	5.25
Cystophora torulosa	804.28 (81)	160.86 (16)	7.5
Durvillaea antarctica	605.73 (85)	121.15 (17)	5.75
Porphyra spp	252.98 (61)	50.6 (15)	1.33

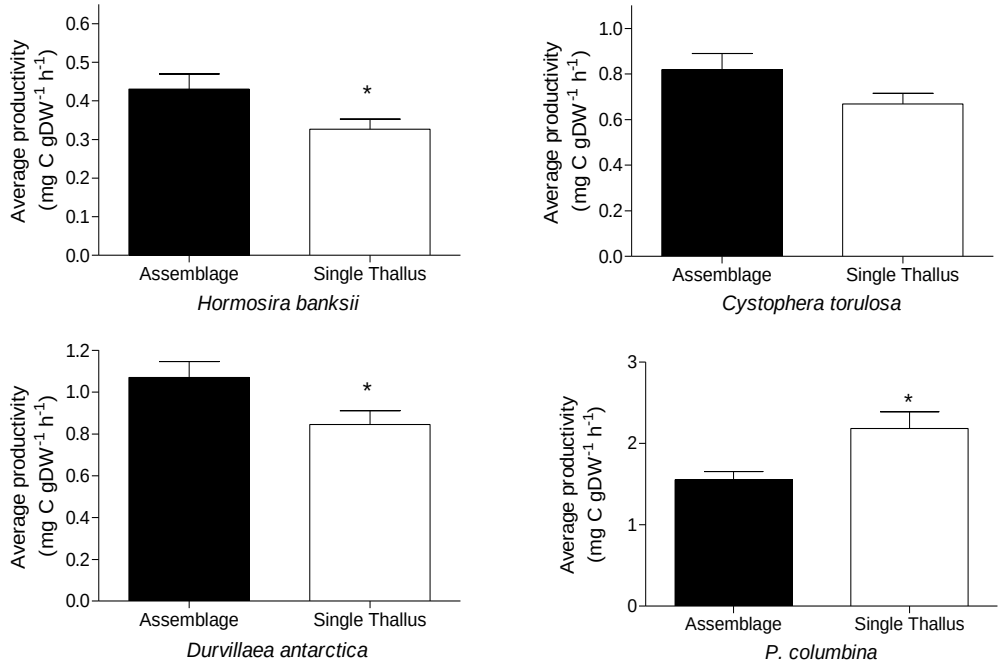

Figure 2.12. Average primary production (±SE) of algal assemblages compared with the dominant species within the assemblage (standardised by gram dry weight of algae). Significant differences indicated by * ($p < 0.05$).

2.3.3. *Effects of canopy removal on primary production dynamics*

H. banksii and the basal assemblage formed the largest proportion of the biomass within these assemblages with an average biomass of 33.34±9.8 g DW and 29.67±2.7 g DW respectively (Table 2.3). *C. torulosa* contributed the least to the assemblage, but had the greatest rate of net photosynthesis of the three components on a per-weight basis (average of 0.76 mg O_2 gDW^{-1} h^{1} at irradiance levels > 500 μmol m^{-2} s^{-1}). The basal assemblage was made up of predominantly *C. officinalis*, with trace amounts of *Champia novae-zelandiae*, *Colpomenia bulosa*, *Leathasia difformis* and *Jania micrarthrodia*.

Intact assemblages had a P-E curve that was very different from the assemblage components, with no indication of saturation of photosynthesis (Fig. 2.13). Net photosynthesis increased throughout the range of irradiance with no sign of photoinhibition, despite *H. banksii* (which showed photoinhibition when incubated alone) being the dominant species. Removal of components had a significant effect on net photosynthesis and there was a significant effect of treatment on all photosynthetic parameters α, γ, R, P_{2000}, and E_c (Table 2.4). Removal of *C. torulosa* from the assemblage

(Fig. 2.13 A) resulted in a slight fall in net photosynthesis throughout most levels of irradiance, but was significantly lower than the intact assemblage at 2000 μmol m^{-2} s^{-1} (Tukey's post-hoc test, $q = 5.7$, $p < 0.01$). In the absence of *C. torulosa*, the assemblage showed photoinhibition at high irradiance, as indicated by the significant difference in γ between the intact assemblage and the minus *C. torulosa* treatment (Tukey's post-hoc test, $q = 8.4$, $p < 0.001$). Removal of both *C. torulosa* and the dominant *H. banksii* resulted in a further fall in primary production and a dramatic change in the dynamics of light use. In particular, there was a change from an almost linear relationship to a saturation curve. Tukey's post-hoc tests revealed that P_{2000} was significantly lower than the intact assemblage ($q = 9.8$, $p < 0.001$), as well as a significant difference in γ ($q = 7.1$, $p < 0.001$). Changing the removal order (Fig. 2.13 B) by removing the dominant *H. banksii* first resulted in a slightly different relationship. Again there was a significant effect of the minus *H. banksii* treatment (Table 3). However, unlike the loss of *C. torulosa*, the loss of *H. banksii* from the assemblage was associated with a steeper increase in net photosynthesis at low irradiance (α) and higher production at 300 μmol m^{-2} s^{-1}, although this was not significantly different from the intact assemblage. There was a significant difference in the compensation point of these two assemblages (Tukey's post-hoc tests, $q = 5.8$, $p < 0.01$). Conversely, net photosynthesis of the assemblage without *H. banksii* was significantly lower than the intact assemblage at 2000 μmol m^{-2} s^{-1} ($q = 4.3$, $p < 0.05$). However, when the basal assemblage was removed first (Fig. 2.13 C), there was very little change in net photosynthesis, and although there was a slight drop at 2000 μmol m^{-2} s^{-1}, this change was insignificant. When both the basal assemblage and *C. torulosa* were removed (leaving only *H. banksii*) there was a larger drop in net photosynthesis at 2000 μmol m^{-2} s^{-1} (Tukey's post-hoc test, $q = 4.3$, $p < 0.05$). Although photoinhibition was seen in single thalli of *H. banksii*, an attached monoculture of *H. banksii* did not show the same fall in production at high irradiance. Interestingly, the loss of *C. torulosa* had less of an impact on production in this treatment, compared to where *C. torulosa* was the first species removed (Fig. 2.13 A). This may be a real effect or could be related to slightly variable biomass of *C. torulosa* within these assemblages. Although the data were adjusted for biomass, higher amounts of the very productive *C. torulosa* could possibly skew results.

Table 2.3. Components and relative biomass of typical mid-shore intertidal assemblage dominated by *H. banksii* (of approximate area 20x20cm) and average primary production per dry biomass of algal material.

Assemblage component	Average dry biomass in 20x20 assemblage in grams (±SE)	Percentage contribution to assemblage (±SE)	Production at 800 μmol m^{-2} s^{-1} (±SE)
Hormosira banksii	33.34 (9.8)	46.3 (10.5)	0.41 (0.08)
Cystophora torulosa	8.95 (1.5)	12.4 (2.2)	0.76 (0.09)
Basal assemblage (Total)	29.67 (2.7)	41.2 (3.5)	0.18 (0.05)
Basal assemblage components			
Corallina officinalis	25.87 (2.0)	34.2 (2.8)	
Champia novae-zelandiae	1.82 (0.3)	2.4 (0.3)	
Colpomenia bulosa	1.53 (0.3)	2.0 (0.3)	
Leathasia difformis	0.4 (0.05)	0.5 (0.08)	
Jania micrarthrodia	0.048 (0.02)	0.06 (0.03)	

Table 2.4. Comparison of photosynthetic parameters between assemblages of various compositions including the average and SE of the initial slope *α*, net photosynthesis at 2000 μmol m^{-2} s^{-1} P_{2000} (mg C gDW^{-1} h^{-1}), respiration *R* (mg C gDW^{-1} h^{-1}), the slope at high irradiance *γ*, and the irradiance (μmol m^{-2} s^{-1}) at compensation E_c (n = 8 for all treatments). Significant differences between assemblages indicated by one-way ANOVA.

	Intact Assemblage	Minus *C. torulosa*	Minus *H. banksii*	Minus Basal assemblage	Basal assemblage	*H. banksii*	ANOVA	
Parameter	Ave (SE)	Ave (SE)	Ave (SE)	Ave (SE)	Ave (SE)	Ave (SE)	p	$F_{5,42}$
P_{2000}	0.37 (0.04)	0.23 (0.04)	0.28 (0.03)	0.29 (0.04)	0.1 (0.05)	0.25 (0.04)	<0.0001	10.11
R	-0.1 (0.02)	-0.05 (0.015)	-0.05 (0.01)	-0.13 (0.04)	-0.04 (0.02)	-0.14 (0.03)	<0.0001	16.18
α	$1E^{-3}$ (0.002)	$9E^{-4}$ (0.002)	$1E^{-3}$ (0.002)	$1.4E^{-3}$ (0.003)	$8E^{-4}$ (0.003)	$2E^{-3}$ (0.002)	<0.0001	10.99
γ	$1E^{-4}$ (0.001)	$-1E^{-4}$ (0.001)	$-5E^{-4}$ (0.001)	$3E^{-5}$ (0.001)	$-1E^{-4}$ (0.002)	$-5E^{-5}$ (0.001)	<0.0001	9.36
E_c	83.00 (0.5)	70.00 (0.4)	46.00 (0.8)	72.00 (0.4)	35.00 (0.8)	69.00 (0.6)	<0.0001	8.40

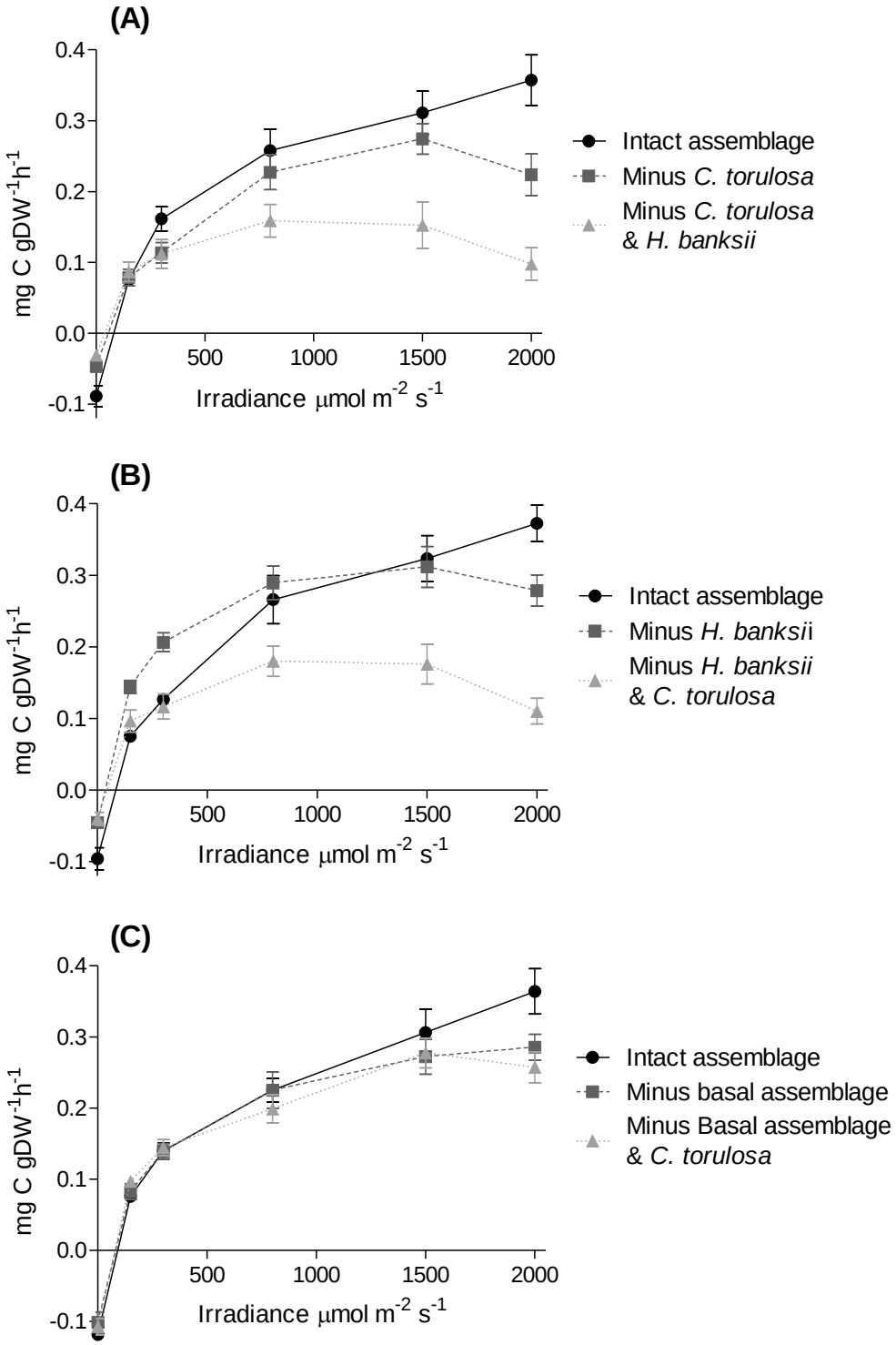

Figure 2.13. Variation in net photosynthesis (±SE) across irradiance levels in different structured assemblages. The removal order varied; A) intact assemblage, minus *C. torulosa*, and minus both *C. torulosa* and *H. banksii*; B) intact assemblage, minus *H. banksii*, and minus *H. banksii* and *C. torulosa*; C) intact assemblage, minus basal assemblage, and minus *C. torulosa*. Net photosynthesis is standardised by dry weight of algae.

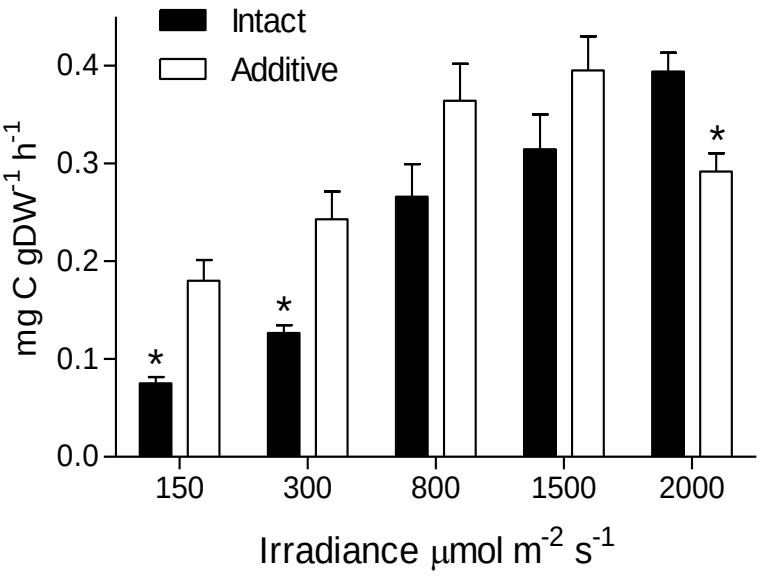

Figure 2.14. Primary production (±SE) of intact assemblage (solid) and additive production (open) against irradiance. Additive production is the sum of the three main components of the assemblage (*H. banksii*, *C. torulosa*, and the *C. officinalis* assemblage) incubated alone. Significant difference indicated by * (p<0.05).

Comparing the production of the intact assemblage to a calculated primary production of the three assemblage components added together showed two very different responses to irradiance (Fig. 2.14). Additive production was the three main components added together as a proportion of their contribution to the assemblage. Additive primary production had a typical saturation relationship and photoinhibition at high irradiance, whereas intact assemblages had a more linear increase in primary production with irradiance. The treatment had a significant effect on production ($F_{1,9}$ = 12.49, p < 0.0001), as did irradiance ($F_{4,9}$ = 29.5, p < 0.0001). There were also clear differences between treatments across the irradiance levels (treatment x irradiance, $F_{4,9}$ = 5.86, P < 0.001). At lower irradiance, the additive production of the components was significantly higher than the intact assemblage (150 μmol m^{-2} s^{-1} t = 2.7, p < 0.05 and 300 μmol m^{-2} s^{-1} t = 3.0, p < 0.05, Bonferroni post-test). At 2000 μmol m^{-2} s^{-1}, however, the intact assemblage was significantly higher than the additive production (t = 2.7, p < 0.05). Production at high irradiance was of particular interest, with the intact assemblage being more productive than the sum of its parts, showing that interactions between the species were enhancing production in the assemblage.

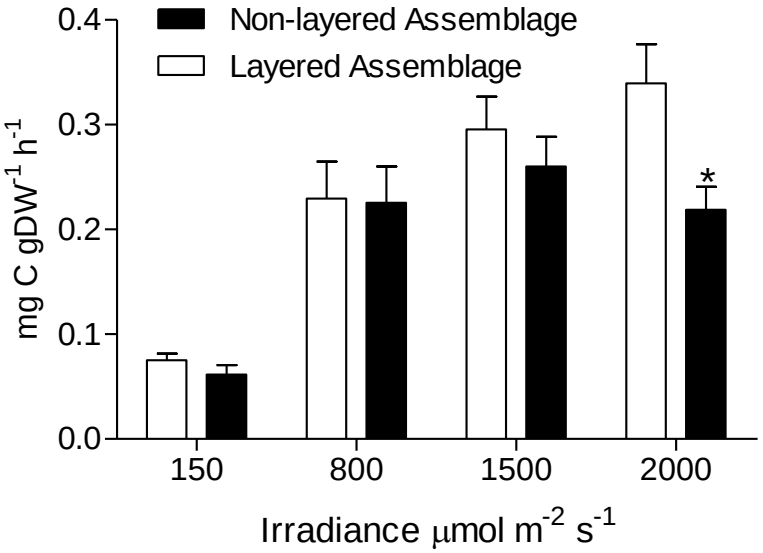

Figure 2.15. Effect of canopy structure on assemblage primary production (±SE) in *H. banksii* dominated communities. Natural intact, layered assemblage (open bars) vs. non-layered assemblage (solid bars) of the same composition. Significant difference in treatments indicated by * (* p < 0.05).

The removal of canopy structure and layering indicates a significant fall in primary production compared to intact assemblages, particularly at high irradiance (Fig. 2.15). Although the species composition was the same, the non-layered assemblage had much lower primary production and also indicates a saturating relationship, as opposed to a linear one (as seen in the intact assemblage). There was a significant effect of treatment ($F_{1,40}$ = 4.5, p < 0.05) and irradiance on production ($F_{3,40}$ = 15.2, p < 0.0001), but no interaction effect. Bonferroni post-hoc tests indicated that the layered assemblage was significantly more productive than the non-layered assemblage at 2000 μmol m^{-2} s^{-1} (t = 4.1, p < 0.05).

2.3.4. *Algal diversity and production*

The natural and manipulated variation in species diversity within the assemblages (Fig. 2.16) had a general trend of increasing production in more diverse assemblages. The strength of this relationship varied with light intensity, with the highest level of irradiance (2000 μmol m^{-2} s^{-1}) showing the greatest production at high diversity and the lowest production at low diversity. The slope of the regression lines became steeper and more significant (greater deviation from zero) with increasing irradiance (800 μmol m^{-2} s^{-1} p <

0.05, r^2 = 0.08, F_{10} = 4.37, 1500 μmol m^{-2} s^{-1}; p < 0.01, r^2 = 0.16, F_{10} = 9.6, 2000 μmol m^{-2} s^{-1}; p < 0.0001, r^2 = 0.49, F_{10} = 46.97). Light intensity had a large effect on the slope of the regression lines with significant differences between the three slopes ($F_{2,146}$ = 5.3, p < 0.01). Two way ANOVA of the data show that species diversity had a significant effect on production ($F_{6,130}$ = 8.7, p < 0.0001), but there was no significant effect of light intensity and no interaction.

The number of canopy layers present in assemblages showed an overall trend of increasing production with increasing canopy complexity (Fig. 2.17) and was further enhanced at higher levels of irradiance. The greatest effect of canopy complexity on production was seen at 2000 μmol m^{-2} s^{-1}, with the highest production at three canopy layers and the lowest production at one canopy layer. Two-way ANOVA showed a significant effect of canopy complexity on production ($F_{2,50}$ = 24.43, p < 0.0001) and a significant interaction between canopy complexity and irradiance ($F_{4,50}$ = 4.8, p < 0.001). Only with three canopy layers was production at 2000 μmol m^{-2} s^{-1} significantly higher than at 800 μmol m^{-2} s^{-1} (Bonferroni post-hoc test, t = 4.6, p < 0.0001). This indicated that canopies of varying complexity were affected in very different ways depending on the amount of irradiance they were exposed to.

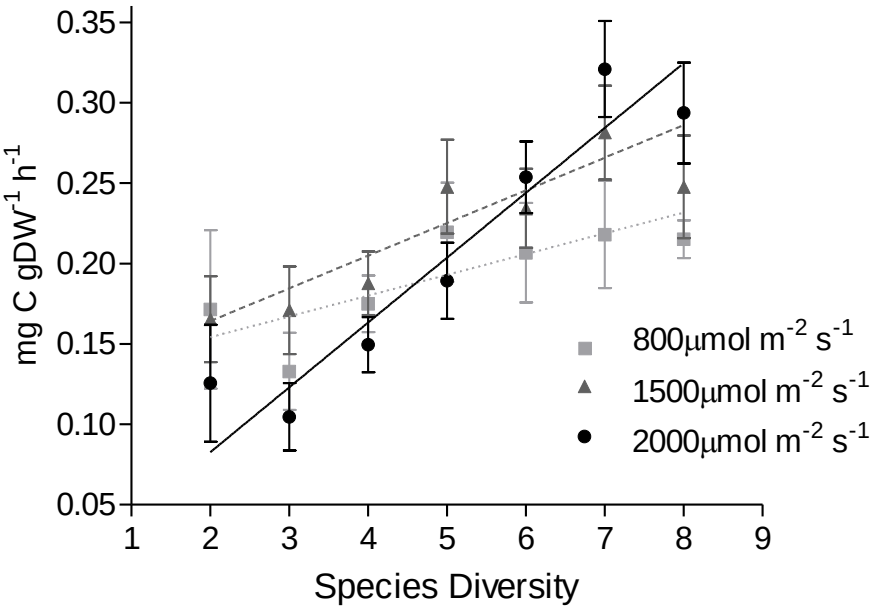

Figure 2.16. Role of algal species diversity on primary production (mg carbon fixed gDW^{-1} h^{-1}) at three levels of irradiance 800, 1500 and 2000 μmol m^{-2} s^{-1}.

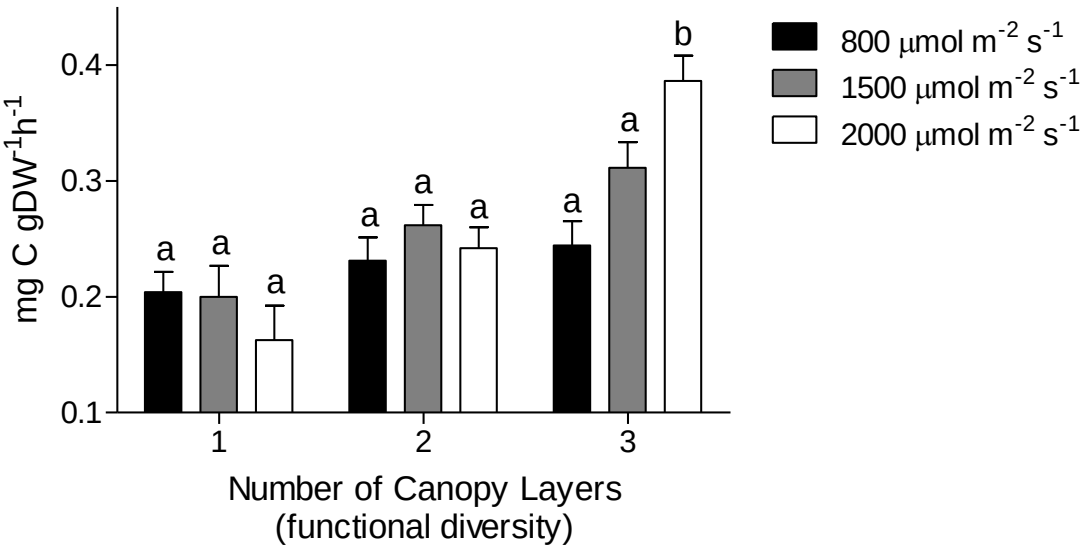

Figure 2.17. The effects of number of canopy layers, or functional diversity on primary production (±SE) at several irradiance levels. Significant difference between groups indicated by different letter using two way ANOVA and Bonferroni post-hoc test.

2.4. Discussion

2.4.1. *Single species primary production*

All the macroalgal species tested in this study show similar P-E curves (i.e., saturation of photosynthesis), but varied significantly in production potential. The four species of fucoid algae showed a general trend of increasing primary production with decreasing shore height with the low-shore species *D. antarctica* and *C. maschalocarpum* showing much higher production than the mid-shore *H. banksii* and the low-shore *C. torulosa*. Also, the irradiance at the compensation point was lower in low-shore species compared to high-shore species, reflecting an adaptation to lower irradiance levels. The consistently lower irradiance levels in the low-shore make it advantageous for algal species in this zone to utilise light of lower irradiance levels more efficiently. This pattern of production is different from those found in some other studies. For example, two studies found greater photosynthetic capacity in high-shore species compared to low-shore species (Gómez et al. 1997; Skene 2004). However, this is most likely due to the use of different functional forms of algae, for example, comparing high-shore foliose ephemeral forms to low-shore fucoid algae. This study, like others, indicates that the foliose forms of algae

such as *Ulva spp.* and *Porphyra spp*. are by far the most productive species on a per area basis and generally occur in the high-shore (Littler & Arnold 1980). Within the same family, however, it seems clear that low-shore genera show higher primary production potential than high-shore genera. Not only is overall production affected by shore height, but the dynamics of light use appears to be related to shore height, with the low-shore species showing much greater light use efficiency at low irradiance levels. This is a typical relationship seen in algae and other autotrophs and reflects an adaptation to low irradiance levels (Lobban et al. 1985). Conversely, the high-shore species showed greater efficiency of light use at high irradiance, with a less pronounced photoinhibition compared to the low-shore species. Similar processes are also exhibited in other species, with sea-ice cover having marked effects on photosynthetic pigment concentration (Aguilera et al. 2002). Macroalgae have been shown to carry significantly higher pigment content before sea-ice break-up compared to after (Aguilera et al. 2002). A similar relationship is likely to occur between high-shore and low-shore adapted species of intertidal reefs in response to light quantity.

The intertidal environment which most of these species inhabit is subject to a range of physiological stressors, in particular temperature, UV radiation and high PAR irradiance. The P-E curves of the higher-shore species reflect this habitat, showing saturation of photosynthesis at relatively high irradiance (MacIntyre et al. 2002). High pigment density in low-light adapted species elevates the risk of oxidative damage caused by reactive oxygen species at high irradiance (Franklin et al. 2003; Hanelt et al. 2003). The photoinhibition exhibited by the high-shore species can only be attributed to PAR irradiance (due to the calibration of the lamp used). Ultraviolet radiation is considered the major driver of photoinhibition, although PAR irradiance is known to cause a reduction in photosynthesis at high levels (Franklin et al. 2003). The reduction in photosynthetic activity is most likely caused by a down-regulation of photosynthetic apparatus, as the short incubation periods were most likely insufficient to cause photosynthetic damage (Häder & Figueroa 1997; Franklin et al. 2003). This down-regulation of photosynthesis is known as 'dynamic photoinhibition,' where photosynthetic oxygen production is reduced to protect the cell from oxidative damage (Häder & Figueroa 1997). The lack of a photoinhibitory effect of high irradiance on *C. torulosa* and *Ulva* sp may suggest that they are unable to down-regulate photosynthesis in the short term, and may be susceptible to higher levels of photosynthetic damage. Although no 'dynamic photoinhibition' is observed in *C. torulosa* and *Ulva lactuca* they could potentially be affected by 'chronic

photoinhibition' under high irradiance regimes. Excess damage to the photosynthetic apparatus over longer periods of high light exposure may lead to a decline in photosynthetic oxygen production and degradation of the reaction centre protein D1 (Häder & Figueroa 1997). This hypothesis is potentially corroborated by the occurrence of an annual burn-off of *C. torulosa* from the intertidal zone over the summer months (Lilley & Schiel 2006), as well as a die-back of *Ulva* sp. in late spring (Schiel & Lilley 2007). Although the die-back of such species may be related to a variety of environmental factors including temperature and UV radiation, it appears that not all species have the mechanisms to regulate excess photo-oxidation and thus may be more susceptible to oxidative damage.

Analysis of single species primary production gives an indication of photosynthetic properties of algae, but tells us little about the interactions which occur in natural assemblages. Although some species may be more susceptible than others to desiccation and burn-off, many species are able to persist beneath canopy forming macroalgae. Amelioration of physical stress by canopy forming species is important for biodiversity and ecosystem functioning in many habitats, particularly the very harsh intertidal environment (Bertness & Calloway 1994; Bertness and Leonard 1997; Lilley & Schiel 2006). Therefore, understanding primary production of complex assemblages will help shed some light on the role of biodiversity and community structure in overall ecosystem function within macroalgal assemblages.

2.4.2. *Assemblage primary production*

In contrast to incubations of single species, an intact assemblage shows a markedly different relationship between production and irradiance. Of particular interest were the differences in the P-E relationships of intact assemblages and their components. The ability to not only maintain production, but increase the rate of production throughout the full range of natural irradiance shows remarkable efficiency of light use. Terrestrial research has shown that the photosynthetic production of leaves does not necessarily represent the production of whole plants (Beyschlag & Ryel 1998) because relative production rates vary throughout the canopy layers and between tissue types. It would, therefore, seem intuitive that the same would hold for marine algal communities which are often comprised of multiple canopy layers. To date, however, the majority of photosynthetic research on marine macrophytes has considered only single species or even single thalli (Flores-Moya et al. 1995; Gómez et al. 1997). Although more recent

studies have examined how light is used in assemblages (Middleboe & Binzer 2004, Arenas et al. 2009), only one (Middleboe & Binzer 2004) found a similar relationship between primary production and irradiance as that seen in this study. The differences in average primary production between an assemblage and its dominant species also suggest that different mechanisms are operating in assemblages compared to single thalli. This is further corroborated when the production of an assemblage is compared to the relative primary production of all its components. Although an assemblage is less productive than its components at low irradiance, at high irradiance it is more productive, showing that an assemblage is not necessarily just the sum of its parts.

The evidence from our study suggests that there is some level of complementarity within marine assemblages. The ability of an assemblage to increase production in a close to linear fashion implies that the role of each component or canopy layer changes in importance at different levels of irradiance. The loss of one or both canopy species leads to a change in the dynamics of photosynthesis. The loss of the less dominant fucoid (*C. torulosa*) had a significant effect on production at high irradiance, which may be related to its lack of photoinhibition at high irradiance and high production potential. Removal of both fucoids affects the linearity of the P-E relationship. Complete loss of the canopy resulted in a change in the dynamics of light use, whereby primary production reverts to a saturation relationship instead of a linear relationship. When the removal order is changed and the dominant fucoid was removed first, the more productive *C. torulosa* enhanced primary production at low irradiance, but due to a change in canopy complexity, production was adversely affected at high irradiance. These results indicate that canopy structure was a very important factor, and should be considered in investigations testing the effects of species diversity on production. The effects of subcanopy species losses show that basal species may be important at high levels of irradiance, but have only a minimal role in primary production at low irradiance where insufficient light penetrates through canopies. Therefore, canopy structure maybe a key factor in testing the role of species complementarity across diversity levels. Random species mixtures, as used in many studies testing the influence of biodiversity on ecosystem function may eliminate the natural layering that occurs within natural canopies of macroalgae and hence will be unable to detect important interactions among species and functional groups, particularly in terms of resource allocation.

Our study leads to the conclusion that layering within macroalgal assemblages plays a major role in maintaining production throughout the natural range of irradiance

and even enhances primary production at high irradiance. Furthermore, it is at high irradiance that canopy complexity has the largest influence on primary production. Although the effect of macroalgal biodiversity on production has been examined (Bruno et al 2005), the role of light intensity has not been extensively tested. Because P-E curves are fundamental to understanding primary production in natural communities, it is essential that they be considered when examining functional relationships in layered communities. The magnitude of the effect of canopy complexity on production is related to the variable light climate to which natural assemblages are exposed. Macroalgae have been shown to have an increased efficiency of light use under fluctuating light in certain cases (Dromgoole 1988, Wing et al. 1993, Kübler & Raven 1996 a & b). Natural variation in irradiance due to canopy movement could significantly enhance the steady state photosynthesis of subcanopy algae. The dominant period of ocean swells is typically within the 5-20 second range, and light flashes of this intensity have been shown to significantly increase light use efficiency in macroalgae (Wing et al. 1993). The delivery of light flecks to the understory during canopy movement may prove to be an important process in overall assemblage production. Flecking of light caused by canopy movement at high irradiance may be an integral part of these systems and could enhance the contribution of subcanopy species. As a consequence, the resource partitioning of assemblages may be misjudged because the main resource for which plant species compete has not been manipulated sufficiently. Despite light being the resource underpinning primary production, many studies testing the effects of biodiversity on ecosystem function have failed to manipulate it in any meaningful way. Although species diversity is not directly manipulated in our study, the important roles of each canopy layer suggest that, to some degree, functional diversity may be essential for overall assemblage production.

This study reinforces the need to examine communities in their naturally structured states as suggested by others (Bracken et al. 2008, Stachowicz et al. 2008) rather than in random assemblages. Although our study was done in controlled laboratory conditions, it considers natural species composition and structure, particularly canopy layering. These results add a new dimension to biodiversity-function research on primary production in the marine environment and indicate the complexity of biological communities. Light, the primary resource for photosynthesising organisms, may prove critical in uncovering an effect of diversity on function within autotrophic communities. Canopy structure and light delivery are vital to subcanopy production within tropical forest ecosystems

(Chazdon & Pearcy 1991; Kursar & Coley 1993; Valladares et al. 1997), and it appears a similar process operates in marine macroalgal assemblages. The delivery of light flecks to the understory during canopy movement may prove to be an important process in overall assemblage production. Of course, this needs further elaboration through *in situ* tests where light delivery may be more complicated. If ecosystems as different as intertidal macroalgal assemblages and terrestrial rainforests show similarities in light use, then canopy structure may play an essential role in the enhancement of primary production at high biodiversity in natural communities.

2.4.3. *Summary*

Dynamics of primary production are significantly different in macroalgal assemblages compared to the individual components of a community. Intact assemblages made up of a variety of species show a more linear relationship between irradiance and production compared to single species, or single thalli. This may have significant implications for biodiversity-ecosystem function research, and shows the potential for diverse assemblages to enhance production *via* complementarity in resource use. Analysis indicates that primary production is enhanced at higher functional diversity, particularly at high irradiance levels. These data indicated that biodiversity and natural canopy structure may be particularly important for ecosystem function at the higher end of resource levels, making it essential to manipulate resource quantity when examining the relationship between diversity and function. This research may help elucidate the mechanisms by which ecosystem function may be enhanced by diversity within autotrophic communities.

In situ primary production

Development and use of a benthic, *in situ*, photorespirometer to measure primary production in macroalgae

3.1. Introduction

Oxygenic photosynthesis is responsible for virtually all biochemical production of organic matter in marine and terrestrial ecosystems. Transfer of energy through most food webs can be directly linked to the fixation of carbon at the primary producer level (Field et al. 1998). It is vital, therefore, to understand the quantity and quality of primary production in various natural assemblages and the factors affecting it. At the global scale, terrestrial net primary production (NPP) is one of the most modelled ecological parameters and is often the primary metric for ecosystem function (Field et al. 1998; Loreau et al. 2001). However, estimations of primary production of the nearshore benthic marine environment are poorly represented in the ecological literature (Stachowicz et al. 2007). Although marine macrophytes make up a small proportion of ocean primary production, they undoubtedly supply a majority of biomass to nearshore ecosystems. Macroalgal subsidies are documented in analyses of stable isotopes, which show that the signature of marine algae extends far outside of areas where they occur, including non-vegetated nearshore areas and terrestrial landscapes (Anderson & Polis 1998; Hyndes & Lavery 2005), intertidal mud flats (Riera & Hubas 2003), offshore communities (Hill et al. 2006) and deep offshore basins (Fischer & Wiencke 1992). Estimating the potential primary production of macroalgal assemblages is essential, therefore, to understanding the role of macroalgae in reef ecology and the transfer of energy through food webs.

Primary production of marine macrophytes has typically been examined using incubations under laboratory conditions (Littler & Littler 1980; Littler & Arnold 1982) or by *in situ* measurements of change in biomass (Mann 1973; Reed et al. 2008). Although both techniques are useful under certain circumstances, they have numerous shortcomings. Laboratory incubations often fail to scale up primary production to that which occurs in nature (Binzer & Middleboe 2005). Furthermore, laboratory incubations are performed under artificial conditions and often use excised tissue of macroalgal specimens (Flores-Moya et al. 1995; Gómez et al. 1997), which do not necessarily give an accurate estimate of production by whole plants. Measurement of change in biomass (or growth increments) is one way to estimate primary production *in situ* and has the potential to predict large-scale variation in production over time. Reed et al. (2008), for example, showed using growth increment techniques that primary production of the giant kelp *Macrocystis pyrifera* depended largely on the foliar standing crop of algae. However, *in situ* measurements of changing biomass can fail to factor processes of natural loss into

estimations of primary production. In order to account for the frequent loss of biomass, it may be better to measure physiological primary production directly in natural assemblages to achieve estimates of benthic primary production, similar to what is common practice for production by microalgae in soft-sediments (Migné et al. 2004).

Estimations of primary production by assemblages are increasingly relevant, given recent research on primary production in assemblages containing natural compositions of species (e.g., Bracken et al. 2008). Levels of primary production seen in diverse communities indicate that photosynthesis does not show a typical saturation curve, as is usually seen in production-irradiance curves for single species (Lobban et al. 1985), but increases in a more linear fashion (Binzer & Sand-Jensen 2002a; Binzer & Sand-Jensen 2002b; Middleboe & Binzer 2004; Binzer & Middleboe 2005). In fact, primary production within diverse assemblages has been shown to increase in a relatively linear fashion with increasing irradiance up to maximum levels of natural irradiance (Middleboe & Binzer 2004). Understanding the dynamics of primary production across a range of irradiances is particularly relevant to intertidal macroalgae, where changes in light regimes can be large over short time spans through changing tidal height and repeated immersion and emersion. Such relationships have important implications for how primary production should be measured in natural assemblages, because they relate directly to how a diverse canopy structure (i.e., layering of algae in natural assemblages), and therefore diversity, may affect an essential function.

To estimate benthic primary production of a natural macroalgal assemblage effectively, it is necessary to have a means of assaying a whole assemblage and not just a species in isolation. *In situ* photorespirometry incubations have been used for several decades (e.g., Carpenter 1985; Chisholm et al. 1990; Cheshire et al. 1996; Golléty et al. 2008), for example in seagrass beds (Moncreiff et al. 1992; Eyre & Ferguson 2002) and other soft sediment systems (Dalsgaard 2003; Migné et al. 2004), presumably because the low profile (i.e., very low standing biomass and short height of autotrophs) of communities and quiescent conditions enable incubation chambers to be readily sealed. Photorespirometry of benthic communities on rocky reefs has received some attention, but incubations have usually been on displaced algae (Littler & Littler 1980, Littler & Arnold 1982; Cheshire et al. 1996), or on algae cultured on settlement plates (Carpenter 1985). Only a few studies have analysed photosynthesis within intact, *in situ* macroalgal assemblages (Chisholm et al. 1990; Golléty et al. 2008; Miller et al. 2009; Noël et al. 2010). The system used by Chisholm et al. (1990) was designed primarily to examine

tropical encrusting turf assemblages, but it was small, at only 50 cm^2. More recently, several studies have used larger chambers, integrating production in whole macroalgal assemblages. For example, Golléty et al. (2008) tested primary production during emersion on *in situ Ascophyllum nodosum*-dominated assemblages. Miller et al. (2009) developed and used a larger chamber for benthic subtidal assemblages. This had a weighted skirt to create a seal with the reef. Also Noël et al. (2010) used an open incubation method to determine production of rockpool communities. With the exceptions of Miller et al. (2009) and Noël et al. (2010), few studies describe physiological *in situ* primary production of macroalgal assemblages during immersion on rocky reefs. Despite some progress, a major impediment has been having an adequate chamber that can be readily attached with an effective seal, be used in multiple conditions from calm to more wave-swept and be re-used on the same assemblages over time.

I wished to account for primary production in intertidal macroalgal assemblages dominated by fucoid algae and with a diverse understory of red and green algae. I needed a device capable of estimating total net primary production and gross primary production using dark respiration, which measurements of growth increments can miss. With this in mind, a novel incubation chamber was designed and tested on natural benthic communities. This chamber, unlike many other photorespirometers, was fitted around attached assemblages and was firmly attached to a reef surface, providing a quick and effective means of analysing net and gross primary production. This provided a platform to examine assemblages at various stages of succession and could also be used to test effects of disturbance on primary production and the subsequent recovery of natural assemblages. I used this device to test the hypothesis that similar assemblages tested *in situ* and using laboratory methods would have similar production dynamics. *In situ* and laboratory methods were tested in analogous incubation chambers to compare any differences in production dynamics.

3.2. Methods

3.2.1 *Photorespirometer design, materials, and deployment*

Primary production of natural macroalgal assemblages was examined *in situ* using custom-built incubation chambers fixed to the substratum of rocky reefs. Chambers were

designed to be secured around established assemblages of benthic intertidal macroalgae, without displacing them. The chambers were made of a clear Perspex tube (of two heights, 25 & 30 cm, to accommodate varying canopy heights), with a clear Perspex attachment plate and lid (Fig. 3.1). They were attached to a reef using a separate base plate to which the main chambers were bolted. The Perspex tubing had a diameter of 25 cm and covered a reef surface area of c. 491 cm^2. The volume of water contained within the chambers was 12.3 L (25 cm height chamber) or 14.7 L (30 cm height chamber).

Before chambers could be effectively fixed to a reef, the area around the target assemblage needed to be cleared of algae and invertebrates. This was done by scraping the substratum with a chisel and a wire brush. Cracks and concavities in the rocky substratum were filled with a two-compound epoxy resin (Expocrete) to ensure that the surface was flat enough to allow a watertight seal. The use of this resin allowed chambers to be re-fitted during subsequent visits, for example to measure successional events. However, for a short-term fix of leakage problems, a silicon sealing compound (window sealant that binds to moist surfaces) can be used to fill in gaps. In either case, a flat base plate (with a central hole the diameter of the Perspex chamber) was placed around the assemblage and sealed to the reef using inset rawl plugs and four, 10 cm long bolts. Base plates were made from 1 cm thick PVC to which a 5 cm thick piece of closed-cell polystyrene foam was glued. When tightened to the reef, the foam compresses and fills slight irregularities in the reef, forming a good seal between the rock and the base plate. Four long, threaded bolts were used to attach the main chamber to the base plate. The seal between a chamber and base plate was maintained using two rubber 'O rings' that compress when the long bolts are tightened (Fig 1A). The use of the base plates was essential to stop flexing from occurring in the main chamber when tightened to an irregular reef surface and the O rings on the main chamber compensate for any slight flexing in the base plate. The lid of the chamber was attached by four long, threaded bolts which extended from the base plate to the lid; the use of wing nuts allowed quick fixing and removal of the lid. The lid itself was a flat piece of Perspex (10 mm thick) with a circular groove lathed into it, to which an O ring or a 2 mm thick piece of closed-cell foam was fitted. Once chambers were filled with seawater for an incubation, the lid could be quickly secured; any slight leaks from the base plate usually stop because of the vacuum created within the filled chamber. Water samples were taken from two taps in the lid, one to take the sample, the other to replace water (if necessary). The taps were fitted

into two hollow, plastic, threaded plugs that were screwed into threaded holes in the lid (Fig. 1A).

To stop boundary layers from establishing during the sampling period, the water within chambers was mixed using a battery-powered bilge pump (made for use in small boats) that pumped c. 800 Lh^{-1} and was fitted so that the chamber was stirred in a circular vortex motion. It was powered by 12-Volt sealed lead-acid battery (a small motorbike battery) housed in a watertight case (Fig. 3.2 A).

Because most P-E curves are done in controlled laboratory conditions, we tested these same species in the laboratory to enable a direct comparison with field incubations. Laboratory incubations were done using the same experimental procedure as *in situ* incubations, and in identical chambers, except with the base fixed to each chamber. Temperature was controlled by immersing chambers in a temperature-regulated water bath (set to 15˚C). Chambers were mixed internally using the same bilge pumps as in the field chambers. P-E curves were generated using five levels of irradiance (150, 300, 800, 1500 & 2000 μmol m^{-2} s^{-1}), with the light generated by metal halide lamps calibrated to PAR (photosynthetically active radiation). Dark respiration was measured in the laboratory by covering chambers to exclude light. For these lab incubations, macroalgae were taken from the field using a hammer and chisel to remove the substratum, to which the macroalgae remained attached. The attached macroalgae were, therefore, at similar densities, biomass and percentage cover as the field assemblage used in incubations. Data from both laboratory and *in situ* conditions were standardised to a benthic surface area of reef (i.e., the section of substratum removed) to allow direct comparisons, as well as in grams dry weight of algal material (gDW) to compare photosynthetic characteristics of the algae. For the purposes of these experiments, algae were harvested following *in situ* and laboratory incubations in order to standardise data by dry biomass of algae.

3.2.2 *Incubation protocol*

Once a chamber was secured to a reef, the effectiveness of the seal was tested by filling the chamber with seawater (during low tide) and looking for any significant leaks (Fig 1B). If the chamber held water when the lid was secured and no bubbles were observed, the seal was deemed adequate to prevent water flux between the chamber and surrounding seawater. Incubations were done while the tide covered the chambers to ensure that the internal temperature remained stable and so prevented the formation of oxygen bubbles, and also to ensure that the light regime was as natural as possible (Fig.

3.2 B). Light intensity and temperature within the chambers were measured throughout experiments using HOBO (Onset Corporation™) data loggers. The loggers were placed on the inside of the chamber lid to measure irradiance reaching the algal canopy. Light intensity was cross-calibrated and regularly checked for accuracy with a LiCor light meter (LiCor LI 192 quantum sensor). Dissolved oxygen concentration within a chamber was obtained by extracting water samples from the tap on the chamber lid using a syringe, and then immediately measuring with a Hach LDO meter (Model HQ40d). To measure production, samples were taken from the chamber at 20-minute intervals. Oxygen production was converted to carbon fixation using a photosynthetic quotient of 1.1 (Kirk 1994). Syringes were kept cool using the surrounding water and were kept in the dark after extraction to limit post-extraction effects on oxygen concentration (i.e., to prevent warming and the formation of oxygen bubbles). Each replicate reef plot was tested across a wide range of natural irradiance, from very dull conditions (approximately 100-300 μmol m^{-2} s^{-1}) to full sunlight (up to 2000 μmol m^{-2} s^{-1}) to gain a P-E curve for the target species or assemblage (n = 4 for each site). For this reason, experiments on a single replicate plot were often done over several days.

Macroalgal assemblages can contain a variety of sessile and mobile invertebrates. To limit their respiration, visible invertebrates were removed from the target area. However, removing all invertebrates from *in situ* assemblages was often impossible because of their small size (some are much smaller than 1 mm) and the presence of overlying algae. Dark respiration of the entire assemblage was measured, therefore, to obtain an estimate of gross primary production. Dark respiration was measured by covering the chambers with a layer of black cloth with an over-lay of tin foil to stop chambers from becoming heated. Following periods of photosynthesis, the relative respiration rate of macroalgae can be substantially elevated, known as photorespiration (Reiskind et al. 1989). Therefore, once chambers were covered they were allowed to settle for 30 minutes before respiration measurements were started to limit photorespiration. Respiration rates recorded during these shaded experiments were also compared to night time samples of respiration and revealed no significant difference. Oxygen concentration was measured every 20 minutes for up to 2 hours.

3.2.3 *In situ photorespirometry experiments*

Incubations were done during austral spring 2007 and summer 2007- 2008 at Wairepo reef, Kaikoura and North reef, Moeraki (c. 400 km apart) on the east coast of New Zealand's South Island. The sites had a similar suite of macroalgal species, but differed in

rock type and wave exposure. Wairepo reef is composed predominantly of sandstone and mudstone, whereas Moeraki is limestone and various conglomerates. Moeraki is exposed to greater and more frequent wave force. Therefore, chambers were used at sites under quite different wave conditions and rock types.

Respiration by invertebrates may potentially have a large effect on measurements of net production due to consumption of O_2. To account for the potential influence of invertebrates that could not be removed *in situ*, a laboratory experiment was designed to test the effects of invertebrate density on overall community respiration. It was difficult to remove all invertebrates from *in situ* assemblages without causing a major disturbance. However, removing all invertebrates in a laboratory experiment was relatively easy. Therefore, the effects of invertebrate density on respiration rates was tested under laboratory conditions. Respiration was measured by covering chambers with a dark cloth to exclude light. Three treatments of invertebrate density were used: 0, 5 and 10 invertebrates per chamber (n = 6). The invertebrate species used were a combination of the trochid snail *Diloma aethiops* and the chiton *Sypharochiton pelliserpentis*. Macroalgae and invertebrates attached to sections of rock were removed from the field and manipulated in the lab. All invertebrates were removed from the substratum and counted. Once all invertebrates were removed, the macroalgal assemblage alone was incubated. After the zero-invertebrate respiration treatment, 5 invertebrates (approximate natural density) removed from the assemblage were added back into the incubation chamber (excluding any micro-gastropods). For the final treatment, the invertebrate density was doubled to 10 invertebrates per incubation chamber. These incubations were done at three temperatures (10, 15 and 20˚C) to examine potential differences in respiration across a range of natural temperatures.

Irradiance and temperature can be extremely variable in the field, particularly in the intertidal environment where the oscillation of the tides leads to extremes in both variables over a daily cycle. It was necessary, therefore, to test the effects of chambers on these parameters relative to ambient conditions outside them. Data loggers were affixed inside and outside of chambers, which were then filled with seawater and fully submerged in an incoming tide during September 2007. Because we wanted to test the greatest potential effects of the chambers on temperature and irradiance, chambers were closed for the duration of the experiment and no seawater was replaced (as would be done during an incubation experiment). Data loggers were set to record at intervals of 10 seconds to capture relatively fine-scale variation in irradiance and temperature.

First, it was necessary to calibrate the chambers to *in situ* conditions. This was done through a series of experiments testing the limitations and effectiveness of the chambers. To understand the limitations of the chambers for measuring oxygen evolution, an experiment was done to test the potential for decline in production over time. The discrete volume of water contained within the chambers has the potential to become depleted in essential nutrients, super-saturated with oxygen during photosynthesis or depleted of oxygen during respiration. If natural conditions were to be measured during incubations it would, therefore, be necessary to replace seawater before a appreciable decline in primary production occurred. To determine the effective time for incubations, we tested the decline in production over time in sealed chambers. This was done on relatively dense stands of *Hormosira banksii* (a fucoid alga reaching approximately 30 cm height and with a biomass of up to 8kg fresh biomass per m^{-2} or approximately 2 kg dry biomass), because an assemblage with large biomass was most likely to saturate. Change in oxygen concentration in chambers was sampled every 20 minutes for 80 minutes at four levels of irradiance: 800, 1000, 1200, and 2000 μmol m^{-2} s^{-1}, with four replicates for each. Following this, the experiment was repeated on the same plots, but with the water inside the chambers being replaced every 20 minutes.

Daily variation in ambient oxygen concentration may cause limitations in primary production of macroalgal assemblages under conditions of minimal mixing. Super-saturation of oxygen under quiescent conditions may cause inhibition of photosynthesis within the algae. Therefore, the variation in ambient oxygen concentration and primary production throughout the day were analysed. Data were collected from several experiments done over different days and under various irradiance regimes. To ensure consistency, data were taken on incoming tides during mid tide when water height ranged between 20-60 cm above the reef. This was done on several days across three weeks during October 2008. Data were collected only on relatively calm days, where super-saturation was most likely. Incubations were done on *H. banksii*-dominated assemblages using the best experimental procedure identified above (i.e., 20-minute incubation duration). Data on ambient oxygen concentrations were collected adjacent to chambers where production measurements were taken.

Production-irradiance (P-E) curves were generated for two species. Monospecific stands were found in natural assemblages and were used to avoid any complications involved with having different compositions of species in replicate plots. The species were *H. banksii* and *Corallina officinalis*, a turf-forming calcareous alga dominant in the

understory of canopies. Incubations were done (n = 4 for each species at each site) between September 2007 and February 2008. However, the curves for the two sites were identical, so results were pooled for presentation. For laboratory incubations, *H. banksii* and *C. officinalis* attached to rocks that were chipped away from the reef surface were collected from the field. These monospecific stands were then bought to the lab where photorespirometry incubations were done. To compare *in situ* and laboratory-based incubations, *in situ* data were pooled into several irradiance ranges (0, 150, 300, 800, 1500 & 2000 μmol m^{-2} s^{-1}), the same as those at which the laboratory algae were incubated. We analysed primary production across an intertidal height gradient using assemblages at three shore heights (high, mid and low). Different canopy species occurred at the various shore heights, with *H. banksii* dominating the high zone, equal cover of the fucoids *H.banksii* and *Cystophora torulosa* in the mid zone, and *C. torulosa* dominating the low zone. There were also several understory species. Diversities of macroalgae, biomass and relative covers of assemblages were also determined at each site. Data were analysed at irradiance levels above 1000 μmol m^{-2} s^{-1} to test differences in maximal production.

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P-E curves were also generated for intact macroalgal assemblages dominated by *H. banksii* using both laboratory and *in situ* methods. These assemblages were comprised predominantly of canopy species *H. banksii*, the basal turf *C. officinalis* and the subcanopy *Cystophora torulosa* (See Chapter 2). *In situ* incubations were done at Wairepo Reef, Kaikoura (n = 6). For laboratory incubations, *H. banksii*- dominated assemblages attached to rocks, were chipped away from the reef surface. These assemblages were then bought to the lab where photorespiration incubations were done. To compare *in situ* and laboratory based incubations, *in situ* data were pooled into several irradiance ranges (0, 150, 300, 800, 1500 & 2000 μmol m^{-2} s^{-1}), the same as those at which the laboratory algae were incubated.

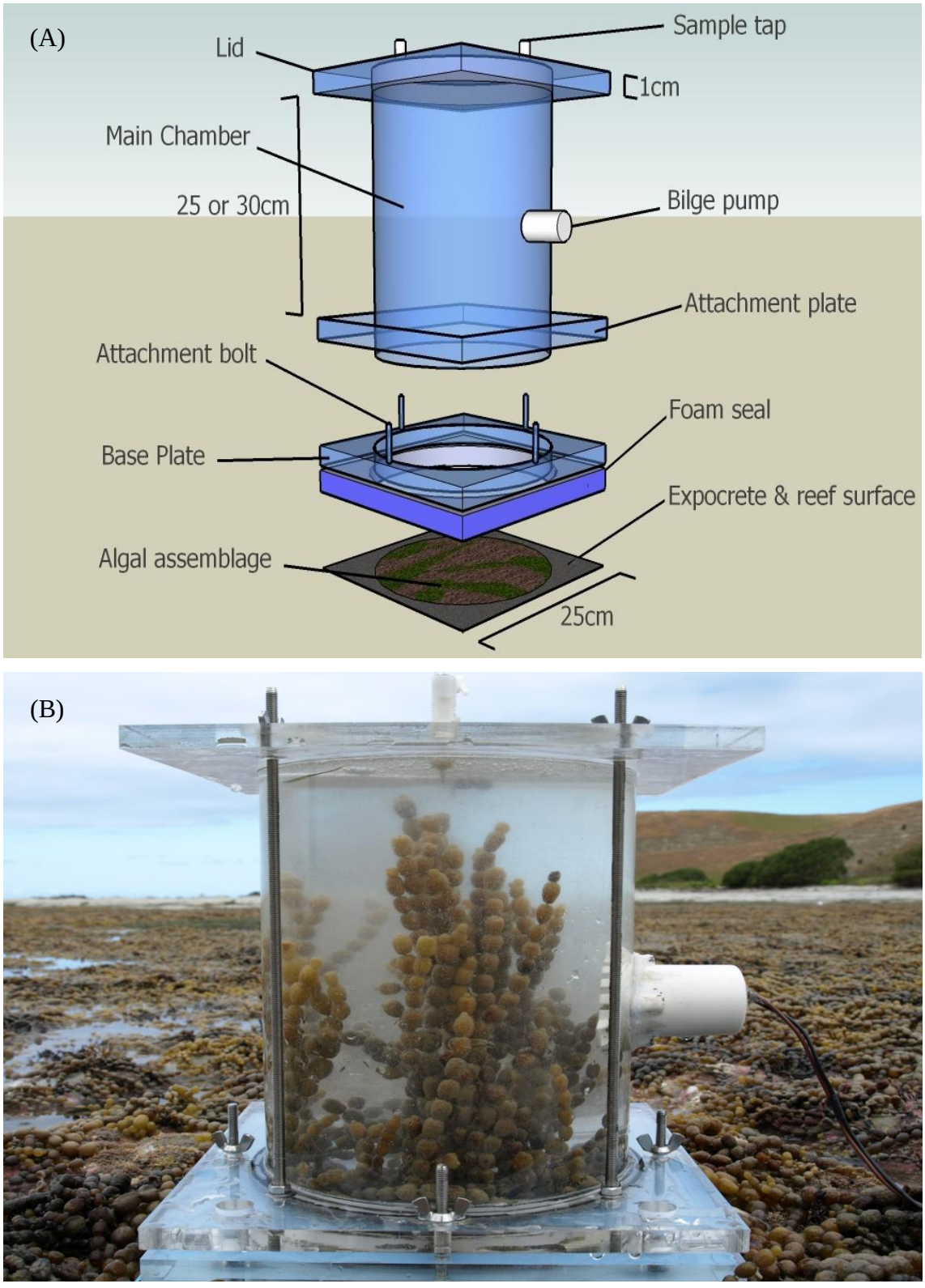

Figure 3.1. *In situ* incubation chamber and its various components: (A) Exploded diagram of components, (B) chamber in place on a reef platform.

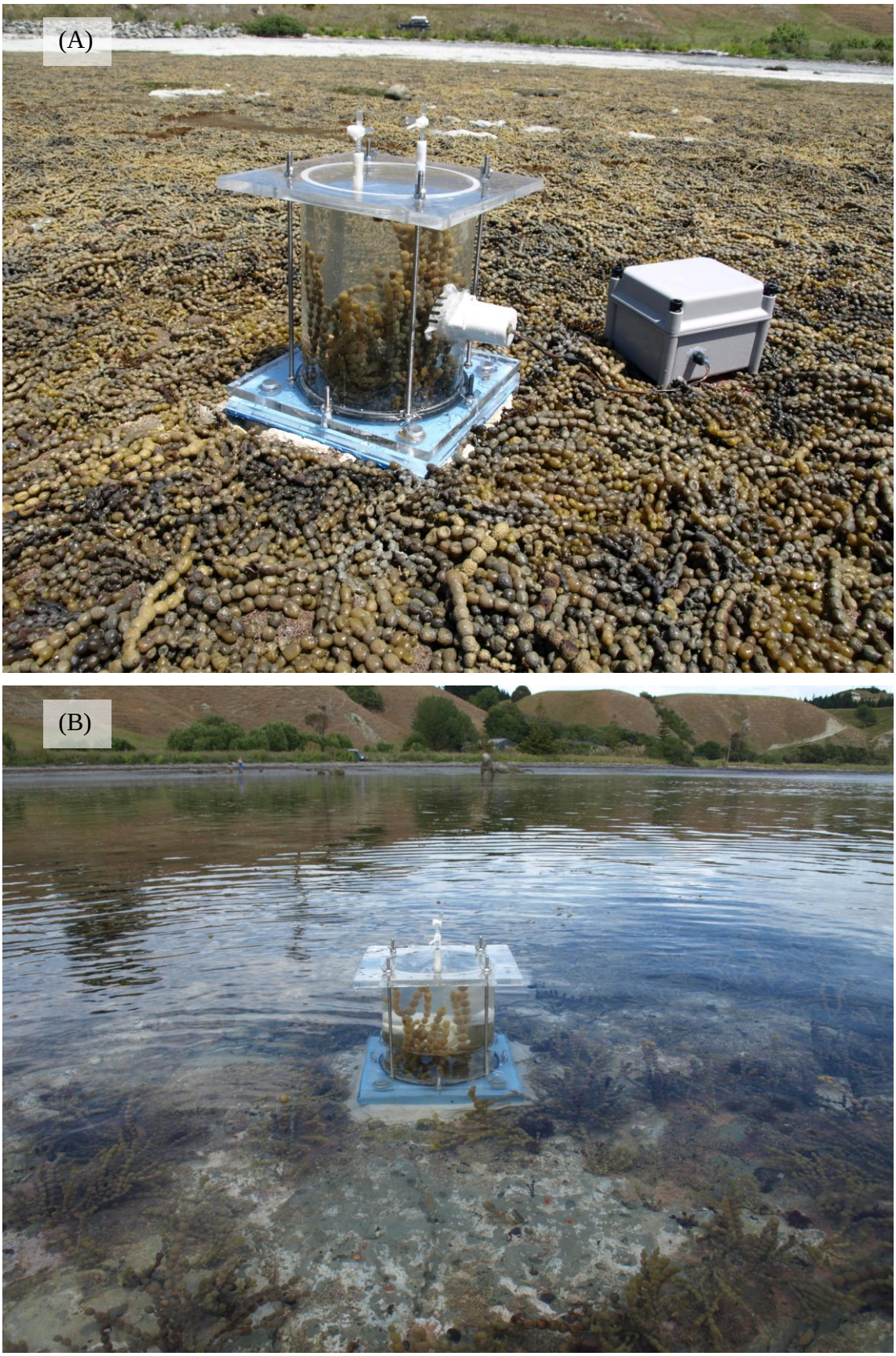

Figure 3.2. *In situ* incubation chamber and waterproof battery housing (A), and incubation chamber under standard incubation conditions i.e. tide partially or fully covering chamber (B).

3.3. Results

3.3.1 *Testing of chambers*

Effects of density of invertebrates *Diloma aethiops* and *Sypharochiton pelliserpentis* on respiration showed a trend of increasing respiration rate with increasing density (Fig. 3.3). Also, respiration rates were increased by elevated temperatures. Although both density and temperature showed a general trend, the results indicate considerable variability, with a large amount of overlap between respiration rates between densities at the same temperature. Two-way ANOVA indicated no significant effect of temperature and no interaction effect, but a significant effect of invertebrate density ($F_{2,45}$ = 4.3, p < 0.05). Invertebrate density has the potential to influence production (i.e., respiration rates affect the net increase in dissolved oxygen), but only with large variations in density.

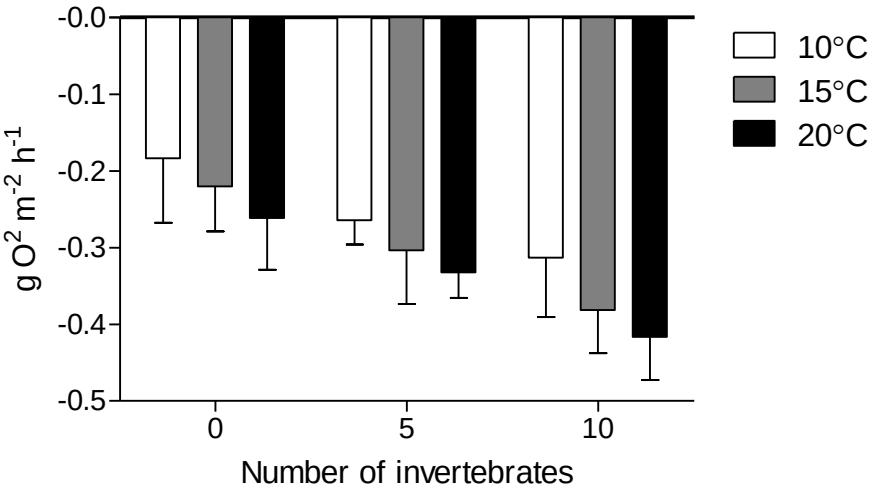

Figure 3.3. Effects of temperature and density of invertebrates on overall respiration (±SE, n = 6) by macroalgal assemblages. Respiration shown at 3 temperatures (10, 15 and 20˚C) and 3 invertebrate densities of invertebrates (0, 5 and 10 per chamber).

When chambers were filled with seawater (which was not replaced at regular intervals) and fully submerged, the internal temperature and irradiance broadly overlapped ambient conditions (Fig. 3.4). Internal and external irradiance levels were similar for most of the six hours of the afternoon and evening. However, there were spikes in irradiance when internal levels were lower than external irradiance, particularly during the spike in irradiance 40 minutes after midday. Beginning at c. 30 min after the start of the experiment, temperatures inside the chamber were c. 1^{o}C greater than those outside. This difference was most pronounced during the warmest part of the day but

disappeared by late afternoon. The spike in temperature at 12:30 was associated with a sharp rise in irradiance. This occurred while the tide was coming in and the chamber was not yet fully submerged. This experiment shows the potential extremes in temperature difference created by the chambers, but under the normal experimental procedure using regular replacement of seawater, this effect would be minimised or eliminated. Even in these extreme conditions, however, irradiance and temperature coincided closely for the first 30 minutes. These data show irradiance and temperature across a single day, but long term irradiance indicate values frequently reaching up to 2000 μmol m^{-2} s^{-1} during sunny days during summer.

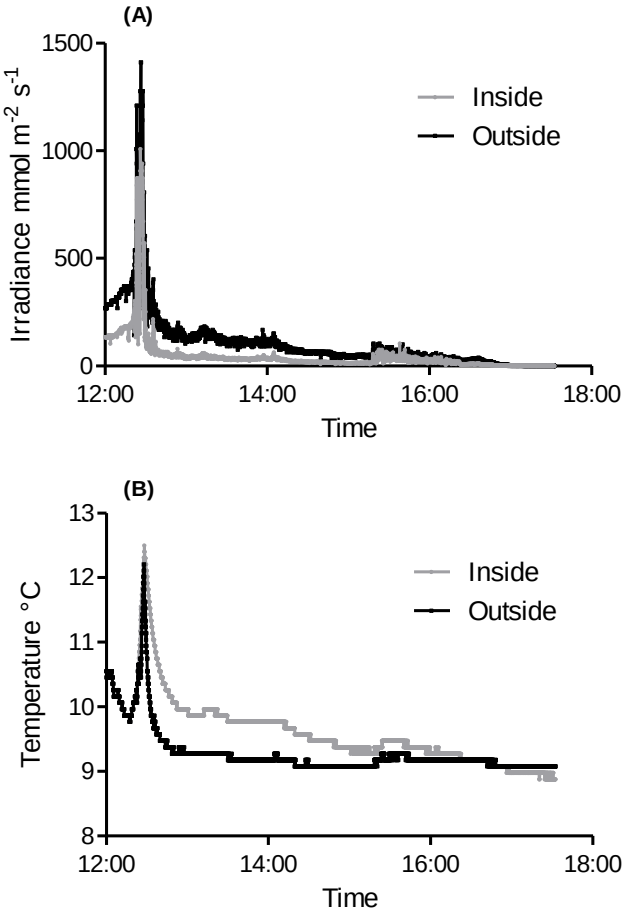

Figure 3.4. Irradiance (A) and temperature (B), inside and outside of the chambers from mid-day to evening during austral spring (on 17 September 2007).

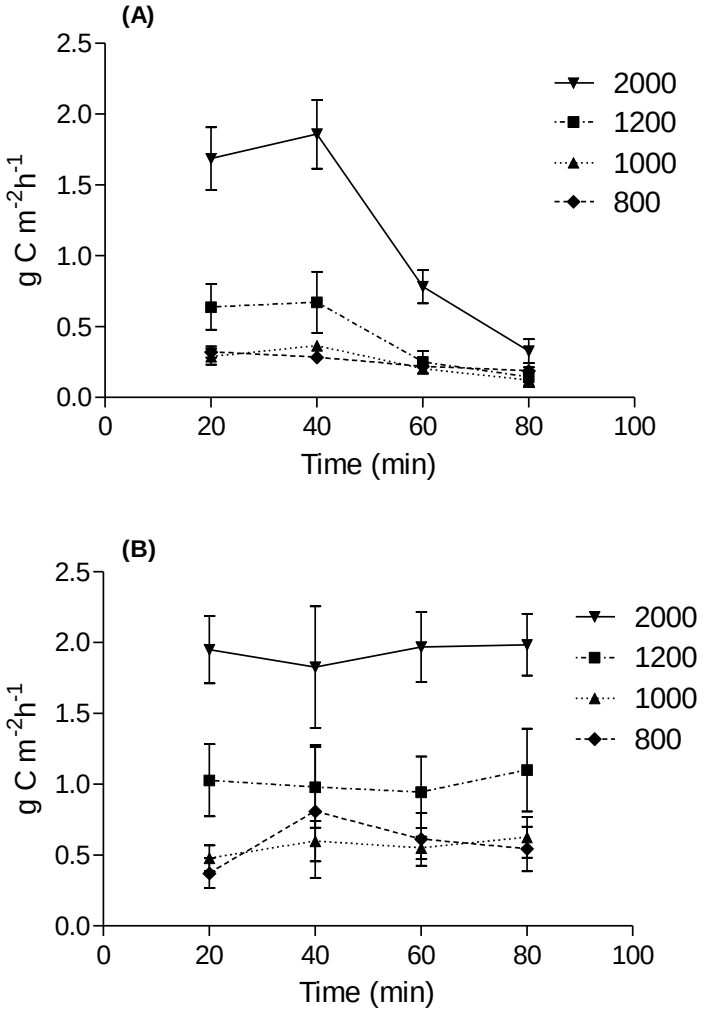

Figure 3.5. Mean net primary production (±SE, n = 4) over time when water is not replaced (A) and when replaced at c. 20-minute intervals (just after each reading) (B) within chambers at various levels of irradiance 2000, 1200, 1000 and 800 µmol m^{-2} s^{-1}.

Tests to determine when primary production began to decline when internal water was not replaced, showed that at 2000 and 1200 µmol m^{-2} s^{-1}, this occurred after 40 minutes (Fig. 3.5 A). Also at high irradiance, the saturation of oxygen reached over 200 % after 60 minutes of incubation time, indicating excessive levels of dissolved oxygen. This effect was less pronounced at lower irradiance levels but still occurred after a similar time. A two-way ANOVA indicated a significant effect of irradiance ($F_{3,48}$ = 221, p < 0.0001), time ($F_{3,48}$ = 97.3, p < 0.0001) and an interaction effect (irradiance x time, $F_{9,48}$ = 27.7, p < 0.0001). Bonferroni post-hoc tests of the data indicated that at both 2000 (t = 10.9, p < 0.0001) and 1200 µmol m^{-2} s^{-1} (t = 4.7, p < 0.016) primary production was significantly less at 60 minutes, compared to 20 minutes. Production at 80 minutes was not significantly less than at 20 minutes in the two lower irradiance treatments (800 and

1000 µmol m^{-2} s^{-1}). However, when seawater was replaced at 20-minute intervals (just after each water sample was taken for analysis), primary production at all irradiance levels remained constant throughout an experiment (Fig. 3.5 B). There was no significant effect of time on production, but there was a significant effect of irradiance ($F_{3,48}$ = 24.19, p < 0.0001). Reliability of results from incubations depends, therefore, on the length of the incubation and the level of irradiance. In particular, at higher irradiance levels, incubations should not exceed 40 minutes, but for efficient sampling, 20 minute intervals would provide greater resolution.

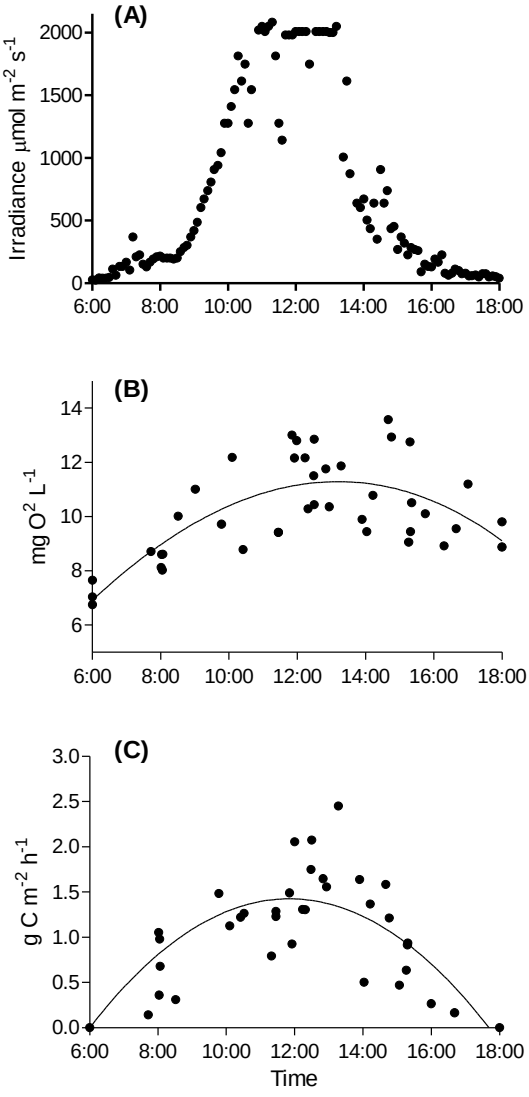

Figure 3.6. Daily cycle of *in situ* irradiance (A), ambient dissolved oxygen concentration (B) and primary production (C). 6:00 is the approximate time of sunrise, 20:00 the approximate time of sunset and between 12:00 noon and 2:00 pm is peak irradiance (during September and October 2007). Lines are fitted using a non-linear regression (third order polynomial, (B) r^2 = 0.52, df = 33, p < 0.0001; (C) r^2 = 0.57, df = 37, p > 0.05).

Daily production data were derived from incubations performed over different days on *H. banksii*-dominated assemblages and compared to daily ambient oxygen concentration across various days. As expected, there was a strong relationship between oxygen evolution and primary production that corresponded to the hours of greatest sunlight (i.e., highest irradiance between 12:00 noon and 2:00pm at 2000µmol m^{-2} s^{-1}; Fig. 3.6). Ambient oxygen concentration generally increased throughout the day, peaked at 14:00-15:00 hours, then declined in the evening. The greatest observed oxygen saturation was 150%, which occurred at approximately 14:00 hours. Primary production showed a similar relationship throughout the day but with a peak between 12:00 and 14:00. Because ambient oxygen concentration increased throughout the day, production late in the day could potentially have been affected by super-saturation of oxygen. However, these data show that the peak in production was related to sunlight rather than to water chemistry.

3.3.2 *Application of chambers*

For both *Hormosira banksii* and *Corallina officinalis*, laboratory data showed saturation at lower levels of irradiance compared to *in situ* data. On a per-area basis, the *in situ* curves reached peak values around 20 % greater than those derived in the lab, and inflection points were at a lower irradiance in the lab (Fig. 3.7 A, C). For *H. banksii*, *in situ* P_{max} was significantly greater when standardized by area (Two-tailed t-test, t = 2.6, df = 7, p = 0.024), but not by biomass. *In situ* P_{max} for *C. officinalis* was significantly greater than laboratory measurements when standardised by area (Two-tailed t-test, t = 3.7, df = 7, p = 0.0036) and by biomass (t = 4.3, df = 7, p = 0.0011). Refraction of light through surface waters *in situ* may have delivered light more consistently through these assemblages than to those in the lab. To control for potential differences in angles of incidence, the laboratory light source was moved to various locations, but this caused no significant difference in primary production. Maximum primary production (P_{max}) of *H. banksii* was almost double that of *C. officinalis* on a per-area basis (Two-tailed T-test, *in situ* t = 6.4, df = 7, p < 0.0001; laboratory t = 5.7, df = 7, p = 0.0002) and on a per dry biomass basis (Two-tailed T-test, *in situ* t = 2.5, df = 7, p = 0.03; laboratory t = 3.7, df = 7, p = 0.004; Fig. 3.7). Since saturation of photosynthesis did not always occur, P_{max} in these monospecific stands was considered as primary production at the highest irradiance analysed (i.e., 2000 µmol m^{-2} s^{-1}). *H. banksii* reached an average *in situ*

production of 1.0 g C m^2 h^{-1}, whereas *C. officinalis* reached levels of 0.5 g C m^2 h^{-1}. Per biomass, both species were in the range of 0.2-0.3 mg C $gDW^{-1}h^{-1}$. Comparisons of the *in situ* and laboratory-derived irradiance curves showed that they were not identical for either species (curves all fitted using one-phase associations).

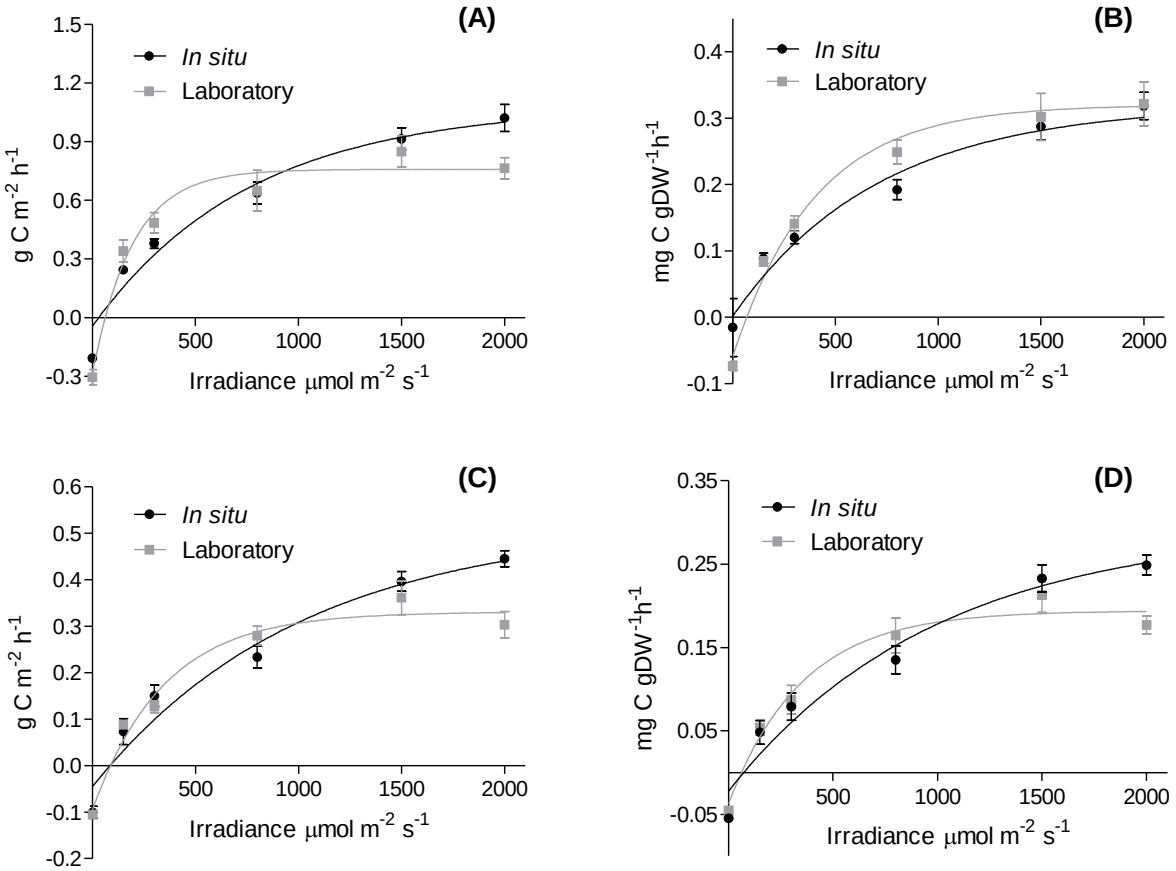

Figure 3.7. Mean net primary production (±SE, n = 8) vs. irradiance (P-E curves) in stands of two dominant species, the fucoid *Hormosira banksii* (A & B) and the calcareous turf *Corallina officinalis* (C & D) under *in situ* or laboratory conditions. Data were standardised in two ways, by surface of reef area (A & C) or by grams dry biomass of alga (B & D).

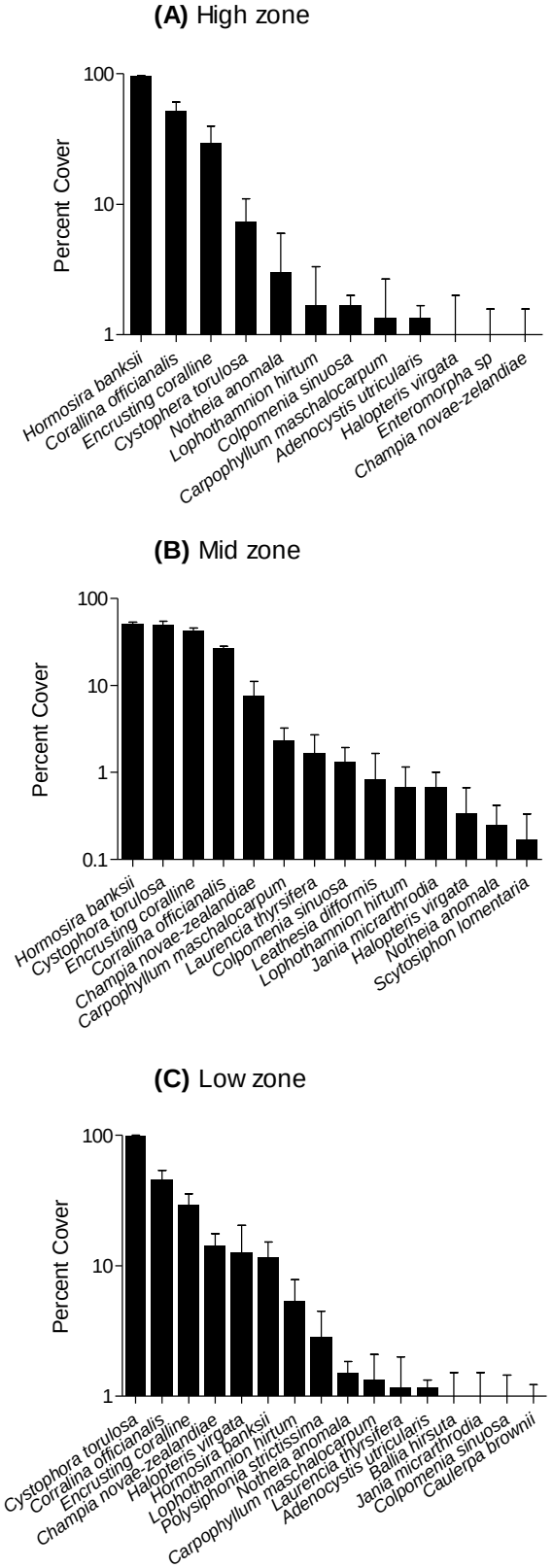

Figure 3.8. Mean percent cover (±SE, n = 3) and number of macroalgal species at three shore heights, (A) high zone *H. banksii* dominated assemblages, (B) mid zone with equal covers of *H. banksii* and *C. torulosa* and (C) low zone *C. torulosa* dominated assemblages. Y-axis shown as log scale.

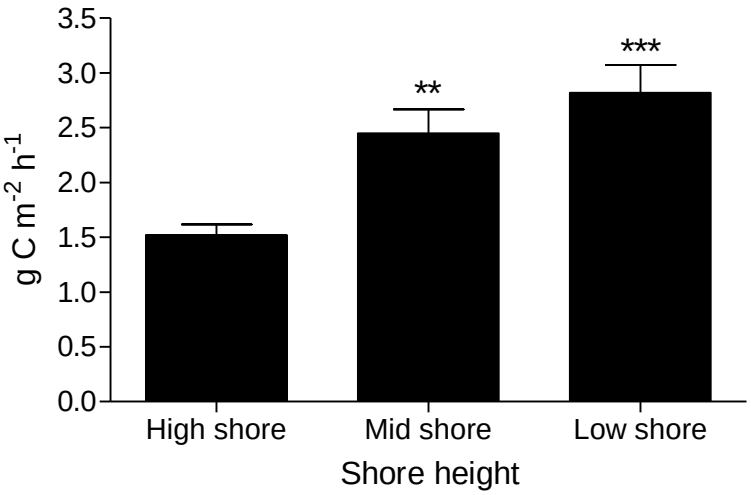

Figure 3.9. Mean primary production (±SE, n = 3) by *in situ* assemblages (Kaikoura, Wairepo) across a gradient of shore height at irradiances above 1000µmol m^{-2} s^{-1}. Significant difference from high shore indicated by (*p < 0.05, **p < 0.01).

Table 3.1. Average dry biomass and average number of macroalgal species in three assemblages dominated by *H. banksii*, equal dominance of *H. banksii* and *C. torulosa*, and *C. torulosa*.

Assemblage dominant	Average dry biomass Kg m^{-2} (SE)	Average species diversity (SE)
H. banksii	2.22 (0.15)	6.33 (0.41)
H. banksii & *C. torulosa*	2.49 (0.29)	7.83 (0.31)
C. torulosa	3.09 (0.32)	8.33 (0.42)

Composition of assemblages down the shore showed a change in the dominance of fucoid species, with the canopy changing from *H. banksii* to *C. torulosa* on the low shore (Fig. 3.8). Generally, the assemblages at each shore height were dominated by *H. banksii*, *C. torulosa* or both, but with a large cover of the turf-forming coralline alga *C. officinalis*. Furthermore, low-shore assemblages had greater numbers of macroalgal species and more species with greater covers. Along with the total number of species, the average number of species and biomass were greater in low-shore assemblages (Table 3.1). There was a clear trend in production down a reef gradient (Fig. 3.9). Primary production at high irradiances (>1000 µmol m^{-2} s^{-1}) was greatest in the low shore assemblage and least on the upper shore ($F_{2,6}$ = 17.8, p < 0.003, One-way ANOVA). Tukey's multiple comparison post-hoc tests showed significant differences between high shore and mid shore (q = 6.1,

$p < 0.05$), as well as high shore and low shore ($q = 8.1$, $p < 0.01$). This gradient in primary production represents a physiological capacity for production only and does not take into account the immersion times at each shore height.

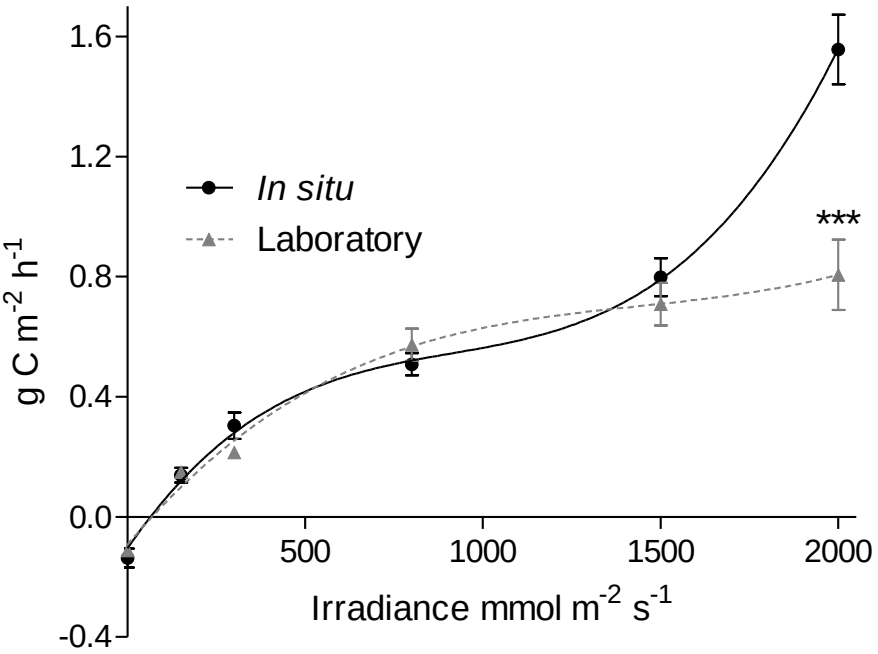

Figure 3.10. P-E (±SE) curves of *in situ* algal assemblages dominated by *H.banksii* (circles) and similar assemblages incubated in the laboratory (triangles). Data are standardised by reef area (g C m^{-2} h^{-1}) Significant difference between laboratory and *in situ* methods indicated by ***, P<0.0001 using two-tailed T-test.

Primary production of *H.banksii* assemblages *in situ* compared to laboratory indicates a similar pattern throughout most the irradiance range (Fig. 3.10). However, at high irradiance (2000 μmol m^{-2} s^{-1}), primary production is significantly higher *in situ* compared to assemblages tested in the laboratory ($t = 4.3$, df = 10, $p < 0.0008$, two-tailed T-test). *In situ* assemblages had different primary production dynamics, in particular, they show a second sharp rise in primary production at high irradiance which is not observed in the laboratory assemblage (curves fitted by third order polynomials *in situ*, $r^2 = 0.85$; laboratory, $r^2 = 0.84$).

3.4. Discussion

As is the case in all complex measurements, certain protocols must be used to ensure reliable results. In particular, the replacement of seawater in the chambers at intervals no longer than c. 40 minutes is essential in preventing a decline in primary production caused either by super-saturation of oxygen or depletion in essential nutrients. Furthermore, temperature control is required in maintaining oxygen in its dissolved form; with insufficient cover of the chambers by surrounding seawater, especially on hot days, the internal temperature quickly exceeds ambient. Although the chambers are well-mixed during incubations there are still limitations in the delivery of nutrients to the contained macroalgae. Wave action and currents would normally provide a relatively constant supply of nutrients to the algal thallus, but when sealed within a chamber, this flux in water is stopped and the algae are completely reliant on nutrients contained within the chamber. Water motion is key to the delivery of nutrients to macroalgae (Hurd 2000; Hepburn et al. 2007), and although the sealed chambers stop transfer of water they are well mixed. Therefore, it is essential that the water, within the chambers is replaced on a frequent basis to avoid declines in nutrients.

A major finding is that there were differences in primary production of similar assemblages tested in the lab and in the field. Field tests showed that readings were consistent and reliable, with variation within less than 10% of the mean (per area) and less than 8% of the mean (per gram dry weight). Reliability of results depends on following the correct procedure, but the data suggest that this is a powerful and reliable technique when used correctly.

These incubation chambers are some of the first documented devices of their kind capable of sealing around large, attached macroalgae on intertidal rocky reefs during immersion. Although many experiments using similar principles have tested primary production on macrophytes *in situ*, they have mostly focused on sediment-based ecosystems (Eyre & Ferguson 2002; Dalsgaard 2003), on macroalgae during emersion (Golléty et al. 2008) or on much smaller algae (Chisholm et al. 1990). One of the major studies on macroalgae attached to hard substrata (Chisholm et al. 1990) fixed the incubation chamber to the reef using masonry tools, which tore away sections of the substratum, and was difficult and time-consuming. Golléty et al. (2008) used a sophisticated incubation chamber that was able to be attached to intertidal rocky reefs, but was only able to measure primary production during emersion. The apparatus used by

Miller et al. (2009), although similar to our device, was used in relatively deep water with the aid of divers. Their chamber was made of flexible teflon sheeting and held down by a weighted skirt around the bottom edge. Although suited to the deep reef conditions it was designed for, it is unlikely to be suitable in the intertidal zone, where frequent wave disturbances would likely dislodge it. The high velocity of water currents in the intertidal zone may also make a weighted seal ineffective at keeping the internal water isolated. Our chambers overcome these problems in the intertidal environment, are a quick (approximately 30 minutes to attach chamber) and effective tool for assaying existing algal assemblages, and involve no major modifications to the reef surface (with the exception of using a small amount of epoxy resin). The ability to seal these chambers around existing assemblages makes it very useful in studying patterns and processes across a diverse range of conditions and habitats and can be repeatedly deployed on the same assemblages.

Our study showed that monocultures of *C. officinalis* can fix approximately 0.1-0.3 grams of carbon per m^{-2} per hour. Chisholm et al. (1990) found that tropical crustose coralline algae had an average *in situ* production of 0.18 g C m^{-2} h^{-1}. Data from our study match this closely, indicating that these techniques produce results comparable across different habitats and reef systems. Primary production by *H. banksii* had a range between 0.3 - 1.0 g C m^{-2} h^{-1} (or approximately 3.3 g C m^{-2} day^{-1}), much greater than that of *C. officinalis*. Production of *H. banksii* monocultures is similar to the gross carbon fluxes of *Asophyllum nodosum* shown by Golléty et al. (2008), at between 0.2 and 0.8 mg C m^{-2} h^{-1}. Average daily production of *Macrocystis pyrifera* was estimated by Jackson (1977) at 9.5 g C m^{-2} day^{-1} (approximately 1.2 - 1.6 g C m^{-2} h^{-1} on average, depending on hours of sunlight) which, as expected by its large size and extensive foliage, is much greater than that of *H. banksii*. Nevertheless, primary production potential of *H. banksii* is within a similar range as that of some large, very productive macroalgae (e.g., Jackson 1977; Golléty et al. 2008).

Differences between laboratory and *in situ* results suggest there are fundamental differences in how light in these two environments may be affecting algae. Probably the most obvious difference between laboratory and *in situ* incubations is the delivery of light, with laboratory light produced by a beam source and irradiance varied by using filters. In contrast, light from the sun can vary significantly from seasonal to second-by-second scales. One clear inconsistency is the change from beam to diffuse irradiance *in situ*, with the presence of cloud cover significantly altering density of shadows through a

canopy. Studies on terrestrial ecosystems suggest that during days of diffuse radiation production may in fact be greater due to the decreased volume of shade within a forest canopy (Roderick et al. 2001). Although this cannot be unequivocally resolved from this study, it does indicate the intricacies of light delivery *in situ* and its importance to production. Furthermore, small-scale fluctuations in irradiance by diffraction through waves adds a further dimension to light delivery in the marine environment. Increasing frequency of light fluctuations is associated with an enhancement of photosynthesis, possibly due to post-illumination bursts of CO_2 (Dromgoole 1988). Variation in irradiance over periods shorter than 1 second can be responsible for the greatest levels of production (Dromgoole 1988), potentially indicating an important role of how light is delivered to macroalgal assemblages.

Variation in primary production with shore height may represent underlying differences among species or possibly differences in assemblage composition and diversity. The pattern observed in this study is different from those found in some other studies. For example, two studies found greater photosynthetic capacity in high shore algae compared to low shore algae (Gómez et al. 1997; Skene 2004). This may be an issue of standardisation, as many studies use dry biomass to standardise primary production, whereas we used surface area of reef (as did Miller et al. 2009), which more directly relates to other ecological processes that are assessed on a per-area basis. Furthermore, these studies considered single species as opposed to whole assemblages. Lower shore assemblages from our study tend to have a greater biomass which is the most obvious explanation for the elevated production at lower shore levels. However, number of species is also greater in low-shore assemblages, suggesting a potential role of biodiversity in the enhancement of production. Structure and composition of assemblages, including diversity and layering, may play vital roles in the dynamics of light use in complex assemblages, and evidence suggests that increasing complexity supports a more linear increase in production with increasing irradiance (as opposed to saturation of production; Middleboe & Binzer 2004; Binzer & Middleboe 2005). Although, this argument is disputable without further research, it does suggest a potential relationship between biomass and species diversity, giving impetus to the argument that diversity may enhance primary production in macroalgal assemblages (Bruno et al. 2005). A greater understanding of how assemblage structure and diversity affect primary production *in situ* may further enhance our understanding of light use dynamics in complex communities.

Entire *in situ* assemblage primary production shows a unique relationship with irradiance, indicating a substantial difference to laboratory based incubations. These results show that there is no saturation of photosynthesis in these complex assemblages, and in fact at very high irradiance, primary production is significantly enhanced. This may indicate very efficient use of light by entire assemblages and a mechanism by which algal diversity could enhance the function of intertidal macroalgal assemblages. Although the exact causes behind the second rise in primary production are not fully understood, it has interesting implications for further research on autotrophic assemblages, and the further use of field based analysis of photosynthesis.

The application of *in situ* techniques can, therefore, extend beyond dynamics of primary production alone. For example, biodiversity-ecosystem function research (BEF) is a developing field in ecology, and research on marine assemblages is relatively scarce compared to terrestrial communities (Stachowicz et al. 2007). *In situ* photorespirometry can be used in experimental conditions where assemblage structure is altered and resultant effects, both spatial and temporal, can be followed through time. Currently, much research has been done in artificial mesocosms (Bruno et al. 2005), but real-world examples will provide new insights to research on function in diverse assemblages (O'Conner & Crowe 2005; Naeem 2006; Stachowicz et al. 2007), including successional processes and recovery of function after various forms of disturbance. These *in situ* techniques can, therefore, be used to test a wide variety of ecological theories pertinent to marine ecosystems.

3.4.1. *Summary*

In this study we have designed and tested a novel benthic *in situ* photorespirometer capable of being fixed to rocky reef habitats. Probably the most significant problem involved with these experiments was the time over which production within the chambers began to decline, making it imperative that internal water is regularly changed. Although replacement of seawater was carried out manually in this study, further development of this apparatus may involve a more automated system of internal seawater replacement as well as internal oxygen recording.

One of the difficult aspects of using these chambers was the initial sealing of the chambers to the reef surface. Many techniques were used to get this right, including the use of small amounts of epoxy resins or silicon seals. However, by far the most effective way of sealing the chambers was finding a flat enough surface to work on. Failing this, using both forms of sealant was very effective. Silicon sealants are fast, cheap and easy to use, and also have the benefit of not being a permanent fixture.

In conclusion, these chambers gave consistent and reliable results and clearly indicated some potential problems involved with lab-based measurements of primary production. Results show that primary production *in situ* is significantly higher than the production measured in the same assemblages under laboratory conditions. Furthermore, the unique inflection point of the *in situ* assemblages suggests that they are able to use light very efficiently, particularly at high irradiance. The applications of this apparatus go far beyond primary production measurement and could be adapted to measure respiration of invertebrate communities.

In situ primary production dynamics

The enhancement of primary production by algal diversity and canopy structure

4.1. Introduction

The global loss of biodiversity has motivated a considerable amount of ecological research over the past decade, testing the role of diversity on various forms of 'ecosystem function.' In particular, the effects of biodiversity on primary production has received considerable attention (Hooper et al. 2005). Despite the intensive research, there is very little agreement among researchers as to the significance of the results generated from these studies (Huston et al. 2000; Loreau et al. 2001; Loreau & Hector 2001; Duffy 2009; Wardle & Jonsson 2010). Positive relationships between species diversity and ecosystem function have been reported in several ecosystems (Loreau et al. 2001; Hooper et al. 2005), yet the mechanisms driving this relationship have been intensely debated (Loreau & Hector 2001), particularly the relative importance of 'complementarity' (effects of resource partitioning on function) and 'selection effects' (effects of sampling productive species on function) in enhancing function. A greater understanding of the relative importance of these two processes has implications for how we view the effects of species loss on ecosystem function. Progress in this area may have been hindered by an almost exclusive use of mesocosm-type experiments, in which species combinations are randomly generated. Evidence suggests that natural communities are far from random and randomly generated species combinations may neglect important interactions occurring in real communities (Bracken et al. 2008). Therefore, if enhancement of function is due to complementarity and the partitioning of resources between species with multiple traits, the greatest chances of detecting it are in naturally structured assemblages. Understanding how real assemblages use resources may give insight into the potential effects of species loss in real-world situations.

It has long been recognised that the primary production of a leaf does not necessarily represent the production of whole plants or ecosystems (Beyschlag & Ryel 1998). Although the role of various canopy layers in terrestrial systems is receiving increased attention due to advances in measurements of CO_2 fluxes (Baldocchi et al. 2001; Mission et al. 2007), understanding the role of various canopy layers in overall primary production has been difficult. The importance of canopy layers on primary production is potentially vital for further biodiversity-ecosystem function research, where the use of 'natural communities' are being called for (Loreau et al. 2001; Stachowicz et al. 2007). Complementarity is an important process in the enhancement of ecosystem function, but selection effects are often stronger (Bruno et al. 2005). However, with

increased duration of biodiversity-function studies, the role of complementarity increases (Cardinale et al. 2007; Fargione et al. 2007), suggesting that longer time-scales allow greater temporal asynchrony and insurance effects. If complementarity is important in mature experimental communities then, by logical extension natural assemblages should be affected by similar processes. However, with few exceptions (i.e., Tylianakis et al. 2008), biodiversity-ecosystem function research in existing natural assemblages has been poorly done. Furthermore, little attention has been given to the role of canopy layering and its effects on primary production in autotrophic assemblages.

Macroalgal assemblages can be comprised of several canopy layers, for example, the giant kelp forests dominated by *Macrocystis pyrifera* often have three canopy layers, the *M. pyrifera* canopy, a subsurface canopy of stipitate kelps, and a understory of articulated and encrusting coralline algae (Reed & Foster 1984). Testing the effects of biodiversity on ecosystem function within naturally structured assemblages should give insight into the relative contribution of species complementarity to the enhancement of ecosystem function. There is evidence that the efficiency of nitrogen use is enhanced at high macroalgal diversity within natural assemblages (Bracken & Stachowicz 2006). Complementarity may also be relevant for light utilisation, whereby functional diversity may enhance production of the entire community (Yachi & Loreau 2007; Vojtech et al. 2008). Understanding light use efficiency in naturally structured and layered assemblages will, therefore, clarify the role of species diversity in enhancing primary production and the mechanism by which this might occur. Canopy layering and functional groups at different canopy heights have long been recognised as important components to total primary production in terrestrial ecosystems, such as temperate forests (Ishii et al. 2009), but no evidence shows a similar role of subcanopy species in marine ecosystems. Furthermore, complementarity in terrestrial assemblages has been shown to be particularly relevant at high resource levels allowing for resource partitioning (Fridley 2002). Uncovering the relationship between biodiversity and ecosystem-function may, therefore, require a greater manipulation of resource quantity. When several canopy layers are present, distribution and use of light is likely to be important to overall assemblage production. Understanding these relationships across a range of assemblage structures will help clarify the role of species and functional groups on function.

Intertidal macroalgal assemblages are good models for testing diversity and canopy effects in autotrophic assemblages. Unlike terrestrial autotrophic assemblages,

production of macroalgae can be easily measured as production of oxygen using photorespirometry chambers (Cheshire et al. 1996; Binzer & Sand-Jensen 2002a; Middleboe & Binzer 2004). Sealing an entire assemblage within a photorespirometry chamber allows the measurement of whole community production over relatively short time scales, enabling a measurement of production at discrete resource levels. To test the role of macroalgal species diversity and canopy structure on assemblage primary production, novel *in situ* incubation chambers were designed and tested on macroalgal assemblages in New Zealand, and Oregon, USA. These allowed for an unbiased assessment of ecosystem function to be made within naturally occurring assemblages of macroalgae and yield estimates of whole community primary production at various levels of a given resource, in this case light. Natural variation in irradiance was used to identify the effects of different levels of resource supply to the macroalgal assemblages. The role of biodiversity was tested using natural variation in species diversity, compared to randomly generated diversity (Bruno et al. 2005) or non-structured assemblages (Bracken et al. 2008) as used in other studies. I tested the null hypothesis that canopy structure and algal diversity had no influence on primary production.

4.2. Methods

4.2.1. *In situ assemblage primary production and contributing components*

Primary production was tested in intact macroalgal assemblages attached to rocky substratum at locations in southern New Zealand, Oregon, and California USA. *In situ* photorespirometers were sealed around numerous macroalgal assemblages using the methods described in Chapter 3. Chambers were sealed around assemblages dominated by the fucoid algae, *Hormosira banksii*, *Cystophora torulosa* (Fig. 4.1) and *Durvillaea antarctica* (New Zealand), as well as *Fucus gardneri* and *Pelvetiopsis limitata* (Oregon, USA). Incubations were done in austral spring/summer 2008-2010 for New Zealand species and in boreal spring/summer 2009 for Oregon species. Incubations of all assemblages included a range of natural irradiances, which were obtained *via* diel variation in light, from low (100 µmol m^{-2} s^{-1}) to high irradiance (2000 µmol m^{-2} s^{-1}). For analysis, primary production (measured by O_2 production) was pooled into irradiance ranges, rather than using a continuous data set for analysis. These ranges were, 0-200, 201-400, 401-800, 801-1200, 1201-1800, >1800 µmol m^{-2} s^{-1}. Data were standardised by

reef area (g C m^{-2} h^{-1}), and/or by dry weight (mg C gDW^{-1} h^{-1}). Dry weight was measured by harvesting macroalgal assemblages after incubations and drying in a conventional oven at 50˚C for 24 hours.

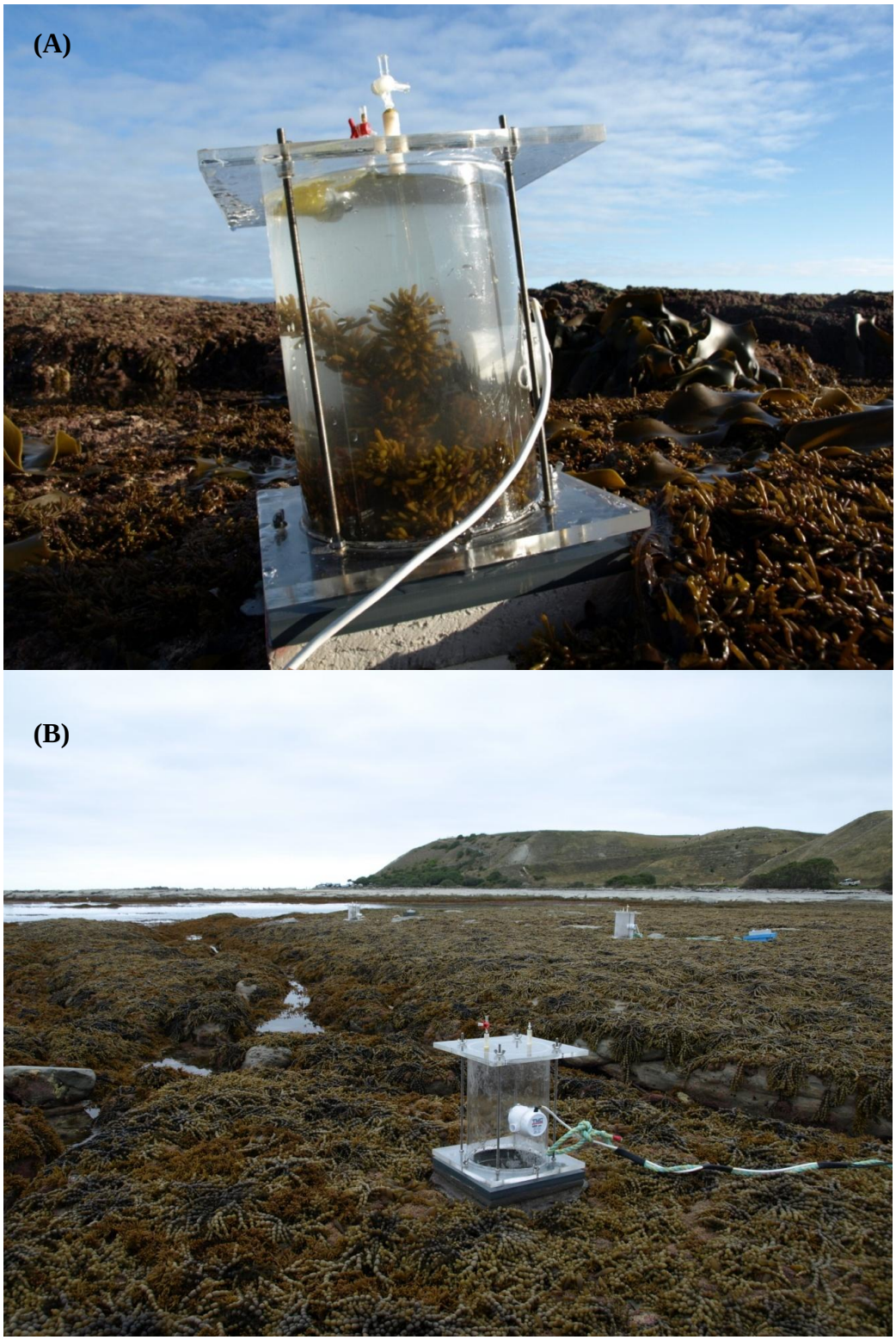

Figure 4.1. *In situ* incubation chamber around an assemblage dominated by *Cystophora torulosa* (A) and three chambers set up on Wairepo reef Kaikoura (B).

To test the assemblage components contributing to overall primary production, various species and canopy layers were removed from *in situ* assemblages. The fucoid-dominated assemblages were comprised of several canopy layers: the main canopy of fucoids, subcanopy fucoids and foliose species, and a basal assemblage of predominantly turf-forming calcareous red algae. Each layer of the canopy was removed to test its contribution to assemblage production (Table 4.1). This was done for assemblages dominated by *H. banksii* in Kaikoura sites and Moeraki, New Zealand, and for *F. gardneri* in Fogarty Creek and Yachats reef, Oregon, USA, with 3 replicates per treatment across all light levels. The removal treatments at Kaikoura were: intact assemblage, minus basal species (predominantly *Corallina officinalis*), minus the subcanopy algae (predominantly *C. torulosa*), and minus the canopy fucoid *H. banksii*. The removal treatments at Oregon were: intact assemblage, minus basal species (predominantly *Mazzaella cornocopiae*), minus the subcanopy fucoid alga *Pelvetiopsis limitata*, and minus the canopy fucoid *F. gardneri*. Removals were not stepwise, so each treatment had only one component removed from it. Production was grouped into two categories of irradiance, low (50-350 µmol m^{-2} s^{-1}) and high (1500+ µmol m^{-2} s^{-1}).

Table 4.1. Single component removal experiments in New Zealand and Oregon. Table shows the dominant species removed in each treatment and the canopy layer at which it occurs.

		Component or species removed	
Treatment	No of replicates	New Zealand	Oregon
Control	3	-	-
Minus Understory	3	*Cystophora torulosa*	*Pelvetiopsis limitata*
Minus Basal species	3	*Corallina officinalis*	*Mazzaella cornocopiae*
Minus Canopy	3	*Hormosira banksii*	*Fucus gardneri*

4.2.2. *In situ PAM fluorometry of subcanopy components*

Pulse Amplitude Modulated (PAM) fluorometry was used to determine photosynthetic characteristics of subcanopy algae at a range of natural irradiance levels. The PAM fluorometer (Heinz Walz GmbH©) was used to measure the effective quantum yield of photochemical energy conversion in photosynthesis. This gives an indication of the comparative photosynthetic state of the algae, but did not give a quantifiable estimate of carbon fixation. The end of the fibre-optic cable was placed at a standard 1cm away from

the algal surface for all measurements, and was always submerged, with care taken to orientate the light sensor correctly (i.e., facing upwards and not shaded by the user). Electron transport rate (ETR) calculated by the fluorometer was used for analyses.

The effects of ambient irradiance (outside canopy irradiance) on subcanopy production was done by placing the PAM fluorometer on several species of subcanopy algae, beneath a *H. banksii* canopy, and measuring their relative ETR. This was done on *Corallina officinalis, Cystophora torulosa*, *Colpomenia sinuosa*, and *Carpophyllum maschalocarpum* at Wairepo Reef and South Bay Kaikoura. An identical experiment was run on macroalgal assemblages in USA using canopies of *F. gardneri*. ETR was measured in *Mazzaella cornucopiae, Mastocarpus papillatus*, *Endocladia muricata* and *Corallina officinalis* on Fogarty Creek, Oregon, and Bodega Bay, California, USA. Data were grouped into three ranges of above-canopy irradiance for analysis. Although, subcanopy irradiance varied, data were grouped into ranges of external irradiance to test the effects of ambient irradiance on subcanopy production. These ranges were, between 0-500, 500-1000, 1000-1500 and 1500+ µmol m^{-2} s^{-1}. To examine the effects of shade on primary production, the ETR of several species were tested below and outside of canopies. In Kaikoura, New Zealand, specimens of *C. torulosa*, *C. maschalocarpum* and *C. officinalis* were found below a canopy of *H. banksii*, and outside of an overlying canopy. In Fogarty creek, and Bodega Bay, USA, specimens of *Rhodomelia larix*, *E. muricata* and *C. officinalis* were found below a canopy of *F. gardneri* and outside of an overlying canopy. Relative ETR between specimens outside and under canopies was analysed at irradiance ranges between 20-100 for New Zealand species and between 50-300 for Oregon species.

4.2.3. *Above and below canopy irradiance dynamics*

To test the amount of light affecting subcanopy production, the light environment in the subcanopy was measured. Four irradiance loggers spaced evenly apart were attached to a weighted ring (25cm in diameter) and then placed around macroalgal assemblages. These irradiance-logging rings were placed around macroalgal assemblages only when water levels were higher than the macroalgal canopy. Loggers were set to record irradiance and temperature at 1 second intervals to determine small scale variation in both parameters. Logging rings were placed around assemblages dominated by *H. banksii* and *C. torulosa* for approximately 2 hours on 6 occasions during summer 2009. Irradiance and

temperature was logged on days of high sunlight, low sunlight and a variety of tidal heights to get a range of conditions. This was done for 4 replicate plots of each dominant species. Furthermore, to relate subcanopy irradiance to surface irradiance, another irradiance logger (also logging at 1 second intervals) was placed on open reef to measure unimpeded irradiance levels. Subcanopy irradiance was calculated by averaging irradiance in the four sub-canopy loggers for intervals of 30 seconds and comparing it to the average surface irradiance over the corresponding 30 second period. From this, a relationship between surface and subcanopy irradiance was derived for the two assemblage types.

4.2.4. *Diversity and primary production*

Natural variation in algal richness was used to analyse the relationship between primary production and biodiversity. In all incubations the number, percentage cover and identity of macroalgal species were recorded. At New Zealand sites, incubations were in the mid tidal zone. Assemblages were dominated by *H. banksii*, and *C. officinalis*, and included a number of less abundant species including *C. torulosa*, *Colpomenia sinuosa*, *Lophothamnion hirtum*, *Adenocystis utricularis*, *Champia novae-zealandiae* and *Carpophyllum maschalocarpum*. Incubations were done over many visits to Kaikoura, at Wairepo Reef and South Bay, and North Reef, Moeraki between 2008-2009. Wairepo Reef was sampled in summer, autumn, winter and spring. South Bay was sampled during summer 2008 and 2009, and North Reef was sampled in autumn and spring. These analyses, therefore, included natural variation in algal richness between and within sites due to recruitment of ephemeral species over time. However, incubations at Oregon sites were not re-visited so they only include variation in species between plots and sites. Incubations were done on assemblages dominated by *F. gardneri* and *P. limitata* and included a number of less abundant species including *Mastocarpus papillatus, Cladophora columbiana, Rhodomelia larix, Endocladia muricata* and *Ulva* sp. All variation in richness at both New Zealand and USA sites is natural variation in species richness within these assemblages.

The relationship between natural variation in functional diversity and production were measured, as well as the effects of non-random removals. This is in recognition that the canopy plants are far more susceptible to removal by storms than the basal species. The cumulative effects of predictable functional group losses were tested by first

removing canopy species, then the remainder of the fucoids, and lastly the removal of all subcanopy species, leaving only coralline turf and encrusting coralline in New Zealand and basal *Mazzaella cornocopiae* in Oregon (Table 4.2). This was done at Wairepo Reef, Kaikoura on assemblages dominated by *H. banksii* and *C. torulosa* and at Foagrty Creek/Yachats Reef, Oregon on assemblages dominated by *F. gardneri* and *P. limitata*. This sequence of removal has been seen following the loss of canopy forming fucoids (Lilley & Schiel 2006), which occurs naturally due to wave force (Underwood 1998; Underwood 1999) and human disturbance (Schiel & Taylor 1999). The cumulative loss of species was done through a series of removals on 5 replicate plots in both New Zealand and Oregon assemblages. The incubations included the following treatments; control, minus canopy species, minus all fucoids, basal assemblage only. This predictable loss of functional diversity was used to examine the effects of non-random species loss on primary production.

Table 4.2. Non-random species removal experiment showing the order of species removal and the number of functional groups remaining.

Order of removal	Number of functional groups	Component removed	
		New Zealand	Oregon
1	4	*H. banksii*	*F. gardneri*
2	3	*C. torulosa*	*P. limitata*
3	2	Understory species	Understory species
4	1	Basal species remaining	Basal species remaining

4.2.5. *Additive partitioning of selection and complementarity*

The relative contribution of selection and complementarity to the enhancement of function was determined using methods developed by Loreau & Hector (Hector 1998; Loreau 1998b; Loreau & Hector 2001). This model separates the net effect of biodiversity into selection and complementarity effects. The selection effect (SE) is calculated by:

$$\mathbf{SE} = \boldsymbol{D} \times \mathbf{cov}(\boldsymbol{M}, \boldsymbol{\Delta RY})$$

Where *D* is the diversity, *M* is the average monoculture biomass and *RY* is the difference between the observed relative yield, defined as *O*, and the expected relative yield, defined as *E*. The effect of complementarity (CE) is calculated by:

$$\mathbf{CE} = \bar{\boldsymbol{M}} \times \boldsymbol{D} \times \overline{\boldsymbol{\Delta RY}}$$

Where $\overline{\Delta RY}$ is the average ΔRY of all the species in a plot, ΔRY is calculated by the difference between, RY_O the observed relative yield and RY_E the expected relative yield. However, these formulae were designed to test the effects of changing biomass on selection and complementarity, which was not the metric of production used in this study. Furthermore, the metric used by Loreau & Hector (2001) and authors using these methods (Fargione et al. 2007; Marquard et al. 2009), is yield, which is based on changes in biomass over time. This is not the best method for determining production of macroalgae (Stachowicz et al. 2007), so in order to use the described methods, slightly different variables were used.

Since the production of individual species in assemblages could not be directly measured as a change in biomass, contribution of species to an assemblage was measured as the difference in production after its removal. Expressed as:

$$O_i = \textbf{Assemblage production} - \textbf{Assemblage minus } species_i$$

The difference between assemblage production and the production of that assemblage after the removal of a given species was used to estimate *O* for each species (denoted as O_i). Production per gram dry weight (mg C gDW^{-1} h^{-1}) at high irradiance was the metric of production used. To define *M*, the production of monocultures of each species was tested, and again were defined as production per gram dry weight of algae. In New Zealand macroalgal assemblages, species were categorised into 4 functional groups, canopy species (*H. banksii*), subcanopy species (*C. torulosa*), basal species (predominantly *C. officinalis*), and ephemeral algae. Due to the low biomass of a range of ephemeral species, they were combined into a single functional group, which is common practice for species with very low biomass (Loreau & Hector 2001; Fargione et al. 2007). Assemblages were categorised into 3 functional groups in Oregon assemblages, canopy species (*F. gardneri*), subcanopy species (*P. limitata*), and basal species (*Mazzaella cornocopiae*, *Mastocarpus papillatus* etc.). These parameters were used to determine the effects of selection and complementarity on production at three levels of functional diversity in New Zealand and two levels of functional diversity in Oregon assemblages.

4.3. Results

4.3.1. *In situ primary production and contributing components*

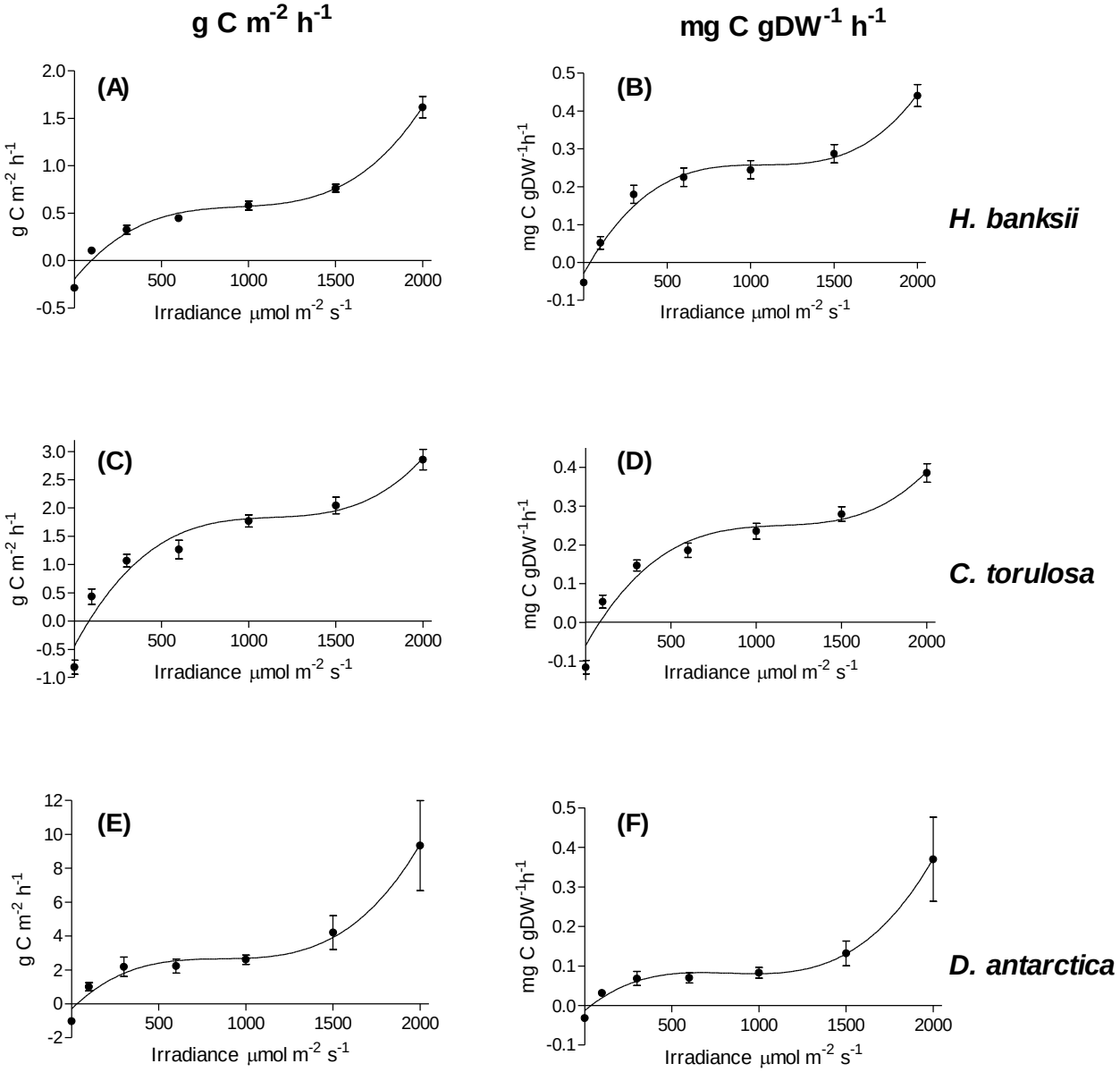

Figure 4.2. ***In situ*** **P-E curves (±SE) for macroalgal assemblages dominated by** ***Hormosira banksii*** **(A and B),** ***Cystophora torulosa*** **(C and D) and** ***Durvillaea antarctica*** **(E and F). Data are standardised by reef area (A, C and E g C m^{-2} h^{-1}) and dry weight (B, D & F mg C gDW^{-1} h^{-1}). Curves were fitted by third-order polynomial functions,** ***H. banksii*** **(A) g C m^{-2} h^{-1}, r^2 = 0.86 and (B) mg C gDW^{-1} h^{-1}, r^2 = 0.85,** ***C. torulosa*** **(C) g C m^{-2} h^{-1}, r^2 = 0.89 and (D) mg C gDW^{-1} h^{-1}, r^2 = 0.87,** ***D. antarctica*** **(E) g C m^{-2} h^{-1}, r^2 = 0.59 and (F) mg C gDW^{-1} h^{-1}, r^2 = 0.71.**

The effects of irradiance on several macroalgal assemblages indicated a two-phase rise in primary production in New Zealand and USA macroalgal assemblages. All curves had an initial rise in production at low irradiance followed by a plateau, before production showed a second major rise at high irradiance (Fig. 4.2, Fig. 4.3). These findings of a second rise in production at high irradiance are novel, and have not been reported for marine autotrophs. In all cases the inflection points occurred at around 1500 µmol m^{-2} s^{-1} which is equivalent to the irradiance on a sunny day.

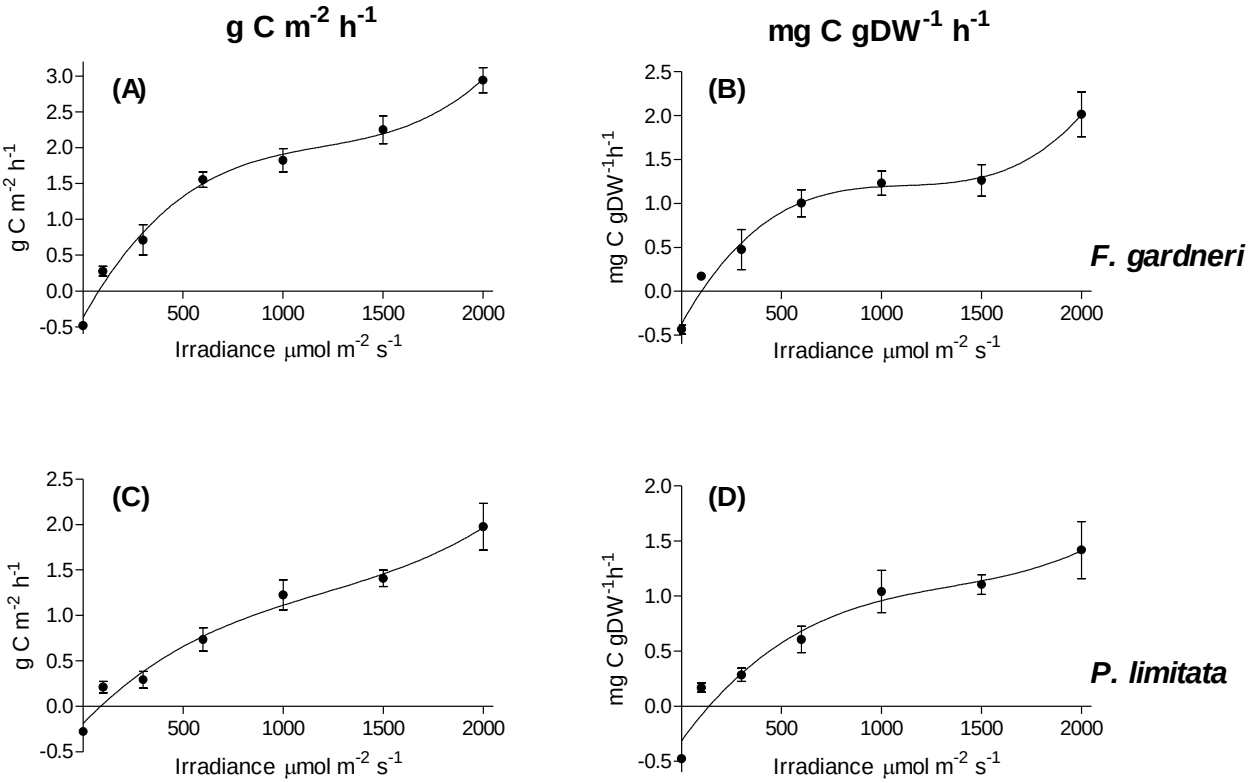

Figure 4.3. *In situ* P-E curves (±SE) for macroalgal assemblages dominated by (A and B) *Fucus gardneri,* (C and D) and *Pelvetiopsis limitata* (Oregon, USA). Data are standardised by reef area (A and C g C m^{-2} h^{-1}) and dry weight (B and D mg C gDW^{-1} h^{-1}). Curves were fitted by third order ploynomials *F. gardneri* (A) g C m^{-2} h^{-1}, r^2 = 0.81 and (B) mg C gDW^{-1} h^{-1}, r^2 = 0.59, *P. limitata* (C) C m^{-2} h^{-1}, r^2 = 0.86 and (D) mg C gDW^{-1} h^{-1}, r^2 = 0.81.

Table 4.3. Results from one-way ANOVA of the effects of irradiance on production, including Tukey's post-hoc test of the difference in production between 1500 and 2000 µmol m^{-2} s^{-1}.

Two-way ANOVA		One-way ANOVA between irradiance levels		Tukey's, difference between 1500 & 2000 µmol m^{-2} s^{-1}	
Species	Unit	p	*F*	p	*q*
H. banksii	m^2	<0.0001	59.9	<0.001	14.1
	gDW	<0.0001	51.8	<0.001	13.1
C. torulosa	m	<0.0001	58.7	<0.01	6
	gDW	<0.0001	53.4	<0.01	5.9
D. antarctica	m^2	<0.0001	8.9	<0.05	5.2
	gDW	<0.0001	13.1	<0.01	6.6
F. gardneri	m^2	<0.0001	32.7	<0.01	5.3
	gDW	<0.0001	11.1	<0.05	4.9
P. limitata	m^2	<0.0001	17	<0.05	5.2
	gDW	<0.0001	14	ns	n/a

One-way ANOVA indicated a significant effect of irradiance on primary production in all assemblages (Table 4.3). Although this was not a surprising result, Tukey's post-hoc comparisons between irradiance levels indicated a significant difference in production between 1500 and 2000 µmol m^{-2} s^{-1} in most cases. Interestingly, the second rise in production significantly increased production compared to pre-rise levels. Production at 2000 µmol m^{-2} s^{-1} was significantly higher than at 1500 µmol m^{-2} s^{-1} regardless of the standardisation unit, with the exception of *P. limitata*, which did not show a significant difference when standardised by dry weight.

Table 4.4. Average species cover and diversity in high, mid and low shore assemblages in New Zealand which were tested for primary production. High shore assemblages dominated by *Hormosira banksii*, mid shore by *Cystophora torulosa*, and low shore by *Durvillaea antarctica*.

	Species cover Ave (±SE)		
Species	High shore	Mid shore	Low shore
Hormosira banksii	96.3 (0.3)	11.6 (0.5)	0
Durvillaea antarctica	0	0	100 (0)
Cystophora torulosa	7.3 (0.8)	99.2 (0.2)	0
Corallina officianalis	51.7 (1.3)	45.8 (0.7)	30 (1.3)
Encrusting coralline	29.3 (1.4)	29.2 (0.7)	41 (1.9)
Colpomenia sinuosa	1.7 (0.3)	0.3 (0.1)	0
Enteromorpha sp	0.3 (0.3)	0	0
Champia novae-zelandiae	0.3 (0.3)	14.2 (0.5)	0
Carpophyllum maschalocarpum	1.3 (0.5)	2 (0.1)	0
Notheia anomala	3 (0.8)	0.2 (0.1)	0
Adenocystis utricularis	0.7 (0.3)	0.2 (0.1)	0
Lophothamnion hirtum	1.7 (0.6)	5.3 (0.4)	0.3 (0.3)
Halopteris virgata	1 (0.4)	12.5 (0.7)	7.3 (1.1)
Polysiphonia strictissima	0	2.8 (0.3)	0
Jania micrarthrodia	0	0.5 (0.2)	8
Laurencia thyrsifera	0	0.8 (0.2)	0
Caulerpa brownii	0	0.3 (0.1)	0
Ballia hirsuta	0	0.3 (0.2)	0.3 (0.2)
Xiphophora gladiata	0	0	0.7 (0.4)
Chaetomorpha coliformis	0	0	1 (0.1)
Codium dimorphum	0	0	0.7 (0.3)
Gigartina decipiens	0	0	1 (0.1)

Cover of dominant fucoid species was close to 100% in all assemblages (Table 4.4, Table 4.5). Diversity of macroalgal species was variable between assemblage types with a total of 13 species found within *Hormosira banksii* plots, 16 in *Cystophora torulosa* plots, 12 in *Durvillaea antarctica* plots, 14 in *Fucus gardneri* plots and 7 in *Pelvetiopsis limitata* plots. New Zealand assemblages were dominated by the canopy forming fucoids, but several other species also reached high cover in the subcanopy (Table 4.4). In contrast, the Oregon assemblages were dominated by the canopy fucoid algae *F. gardneri* and *P. limitata*, with very low cover of subcanopy species (Table 4.5). Diversity was relatively high in *F. gardneri* plots, but very low in *P. limitata* plots with only 7 species found.

Table 4.5. Average species cover and diversity in high and mid shore assemblages in Oregon which were tested for primary production. High shore assemblages dominated by *Pelvetiopsis limitata*, and the mid shore by *Fucus gardneri*.

	Species cover	
Species	High shore	Mid shore
Fucus gardneri	4 (0.5)	96.3 (0.4)
Endocladia muricata	1.75 (0.2)	8.5 (0.6)
Mastocarpus papillatus	5 (0.5)	5.7 (0.5)
Mazzaella cornucopiae	2.5 (0.6)	4 (0.4)
Pelvetiopsis limitata	92.25 (0.8)	1.5 (0.2)
Cladophora columbiana	0	1.7 (0.2)
black non-geniculate	0	1 (0.2)
Ulva spp	1.25 (0.3)	4.8 (0.4)
Rhodomela larix	0	7.3 (0.6)
Odenthalia oregona	0.25 (0.2)	0.3 (0.2)
Porphyra spp	0	0.3 (0.2)
Ceramium eatonianum	0	0.3 (0.1)
Corallina vancouveriensis	0	0.5 (0.2)
Halosaccion glandiforme	0	0.5 (0.2)

The loss of assemblage components indicated that although most species or functional groups are important for production, the canopy species contributed the most to production, even when standardised by dry weight (Fig. 4.4). The loss of *H. banksii* showed that it contributed approximately 50% of overall assemblage production at high irradiance. The removal of *C. torulosa* and the basal assemblage each caused a 25% decrease in assemblage production at high irradiance. Overall, species loss had a greater impact at high irradiance, with very little difference between treatments at low irradiance. Two-way ANOVA shows a significant effect of irradiance (g C m^{-2} h^{-1}, $F_{1,29}$ = 279, p < 0.0001; mg C gDW^{-1} h^{-1}, $F_{3,31}$ = 73.5, p < 0.0001) and treatment (g C m^{-2} h^{-1}, $F_{3,29}$ = 41, p < 0.0001; mg C gDW^{-1} h^{-1}, $F_{3,31}$ = 14.5, p < 0.0001) on production. There was also an interaction effect of treatments across irradiance (treatment x irradiance, g C m^{-2} h^{-1}, $F_{3,29}$ = 16.3, p < 0.0001; mg C gDW^{-1} h^{-1}, $F_{3,31}$ = 6.7, p < 0.0001). Bonferroni post-hoc tests showed that the removal of basal species and the subcanopy *C. torulosa* had a similar effect on production compared to control assemblages (basal species, g C m^{-2} h^{-1} and mg C gDW^{-1} h^{-1} respectively, t = 5.7, p < 0.001, t = 5.1, p < 0.001; minus *C. torulosa* t = 5.2, p < 0.001, t = 6.4, p < 0.001). The loss of *H. banksii* caused a more sizeable drop in production at high irradiance compared to controls (minus *H. banksii* g C m^{-2} h^{-1}, t = 12.5, p < 0.001; mg C gDW^{-1} h^{-1}, t = 9.2, p < 0.001). The loss of *C. torulosa* and *H. banksii*

also significantly reduced production compared to controls at low irradiance, but only when standardised by reef area (*C. torulosa*, t = 2.6, p < 0.05; *H. banksii*, t = 3.1, p < 0.01).

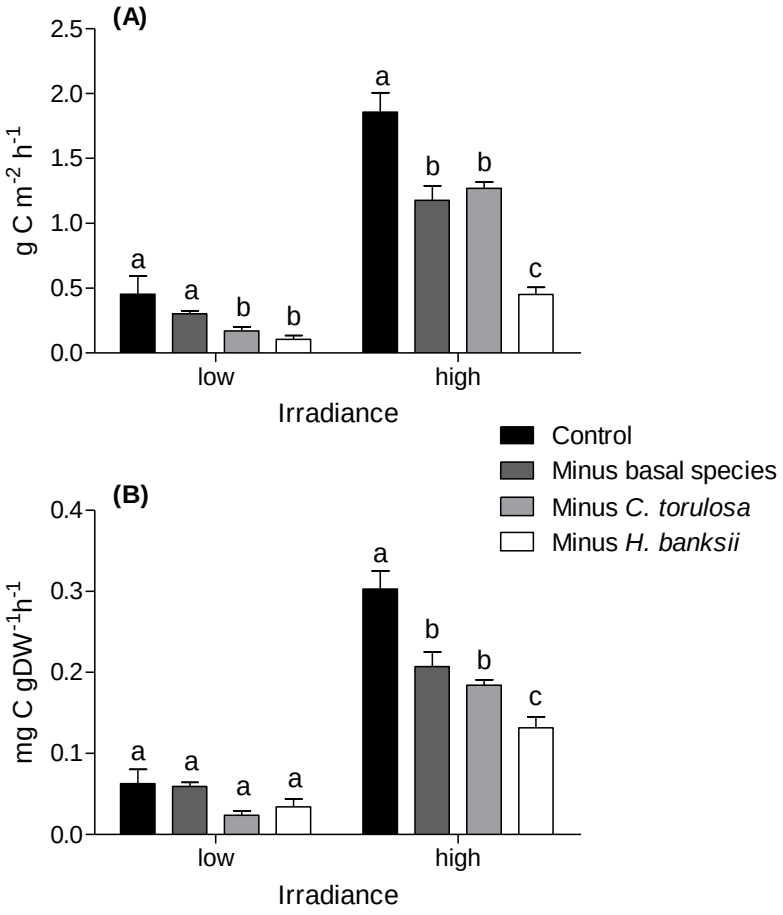

Figure 4.4. The role of several canopy layers on overall primary production (±SE) of assemblages dominated by *H. banksii* at two irradiance levels (high 1500+ and low 50-350 µmol m^{-2} s^{-1}). Significant difference between groups indicated by different letter using two way ANOVA and Bonferroni post-hoc tests. Data are standardised by reef area (A) g C m^{-2} h^{-1}, and dry weight (B) mg C gDW^{-1} h^{-1}.

Removal of various assemblage components from *F. gardneri* assemblages indicated a minimal role of the subcanopy *P. limitata* and basal species, with the removal of the canopy causing the largest decrease in production at high irradiance (Fig. 4.6). However, at low irradiance the species removed had very little effect on production when standardised by reef area (Fig. 4.5 A), and when standardised by dry weight, species removal lead to a rise in production, although statistically insignificant (Fig. 4.6 B). When standardised by reef area, two-way ANOVA showed a significant effect of treatment ($F_{3,8}$ = 8.3, p < 0.0001) and irradiance ($F_{1,8}$ = 84, p < 0.0001). There was also a

significant effect of treatment across irradiance (treatment x irradiance, $F_{3,8}$ = 6.2, p < 0.001). When standardised by dry weight, there was no significant effect of treatment, only an effect of irradiance ($F_{1,8}$ = 73, p < 0.0001). Bonferroni post-hoc tests showed that at high irradiance the removal of *P. limitata* caused a significant fall in production compared to controls when standardised by reef area (t = 6.5, p < 0.001). The removal of *F. gardneri* caused a significant fall in production at high irradiance compared to controls regardless of standardisation (reef area, t = 6.5, p < 0.001; dry weight, t = 2.7, p < 0.05).

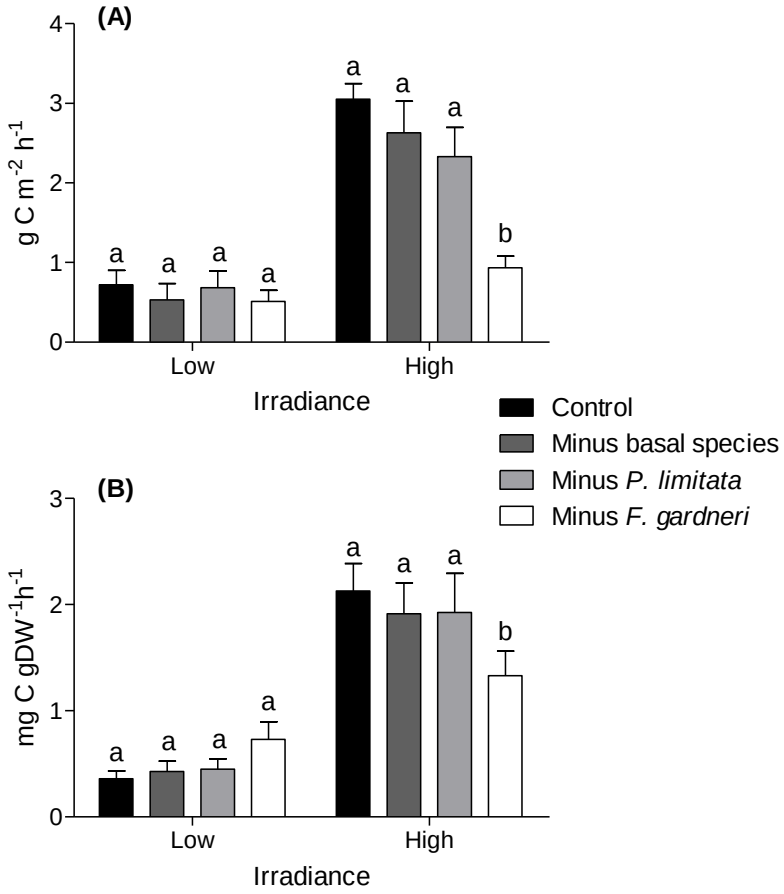

Figure 4.5. The role of several canopy layers on overall primary production (±SE) of assemblages dominated by *F. gardneri* at two irradiance levels (high 1500+ and low 50-350 µmol m^{-2} s^{-1}). Significant difference between groups indicated by different letter using two way ANOVA and Bonferroni post-hoc test. Data are standardised by reef area (A) g C m^{-2} h^{-1}, and dry weight (B) mg C gDW^{-1} h^{-1}.

4.3.2. *In situ PAM fluorometry of subcanopy components*

PAM fluorometry confirmed the effect of canopy structure on subcanopy production (Fig. 4.6 A). For two fucoids (*C. torulosa* and *Carpophyllum maschalocarpum*), one basal coralline (*Corallina officinalis*) and one ephemeral brown alga (*Colpomenia sinuosa*),

electron transfer rate was significantly enhanced with increasing ambient irradiance. In all cases, electron transport rates (ETR) at ambient irradiance levels above 1500 µmol m^{-2} s^{-1} (the approximate point of inflection) were significantly higher than at lower ambient irradiance (Two-way ANOVA, $F_{2,20}$ = 33.5, $p < 0.0001$). There was no significant difference in ETR between 500-1000 and 1000-1500 µmol m^{-2} s^{-1}, suggesting that the change in ETR between 1000-1500 µmol m^{-2} s^{-1} and 1500+ µmol m^{-2} s^{-1} was much larger than the change in ETR from 500-100 µmol m^{-2} s^{-1} to 1000-1500 µmol m^{-2} s^{-1}. ETR at 1000-1500 µmol m^{-2} s^{-1} was significantly lower than at 1500+ µmol m^{-2} s^{-1} in *C. torulosa* (t = 4.3, $p < 0.001$), *C. officinalis* (t = 3.6, $p < 0.01$), and *C. maschalocarpum* (t = 2.8, $p < 0.05$). ETR at 500-1000 µmol m^{-2} s^{-1} was significantly lower than at 1500+ µmol m^{-2} s^{-1} in *C. torulosa* (t = 4.5, $p < 0.001$), *C. officinalis* (t = 4.5, $p < 0.001$), *C. maschalocarpum* (t = 3.9, $p < 0.001$) and *C. sinuosa* (t = 2.7, $p < 0.05$).

The relative Electron Transport Rates (ETR) of several subcanopy macroalgal species from Oregon at increasing levels of ambient irradiance showed much the same relationship as New Zealand species (Fig. 4.6 B). The ETR was significantly higher above 1500 µmol m^{-2} s^{-1}, than at lower ambient irradiance ranges for all species. Two-way ANOVA showed a significant difference between species ($F_{3,25}$ = 8.8, $p < 0.0001$), and a significant effect of irradiance ($F_{2,25}$ = 77.7, $p < 0.0001$). Furthermore, as in New Zealand algae, there was no significant difference in ETR between the lower irradiance levels 500-1000 µmol m^{-2} s^{-1} and 1000-1500 µmol m^{-2} s^{-1} in all species except *E. muricata*, indicating a non-linear increase in ETR with increasing ambient irradiance. ETR was significantly higher at 1500+ compared to 1000-1500 µmol m^{-2} s^{-1} (*M. cornocopiae*, t = 4.6, $p < 0.001$; *M. papillata*, t = 3.5, $p < 0.01$; *E. muricata*, t = 6.0, $p < 0.001$; and *C. officinalis*, t = 3.4, $p < 0.01$) and 500-1000 µmol m^{-2} s^{-1} (*M. cornocopiae*, t = 6.0, $p < 0.001$; *M. papillata*, t = 4.5, $p < 0.001$; *E. muricata*, t = 8.9, $p < 0.001$; and *C. officinalis*, t = 5.2, $p < 0.001$) in all species.

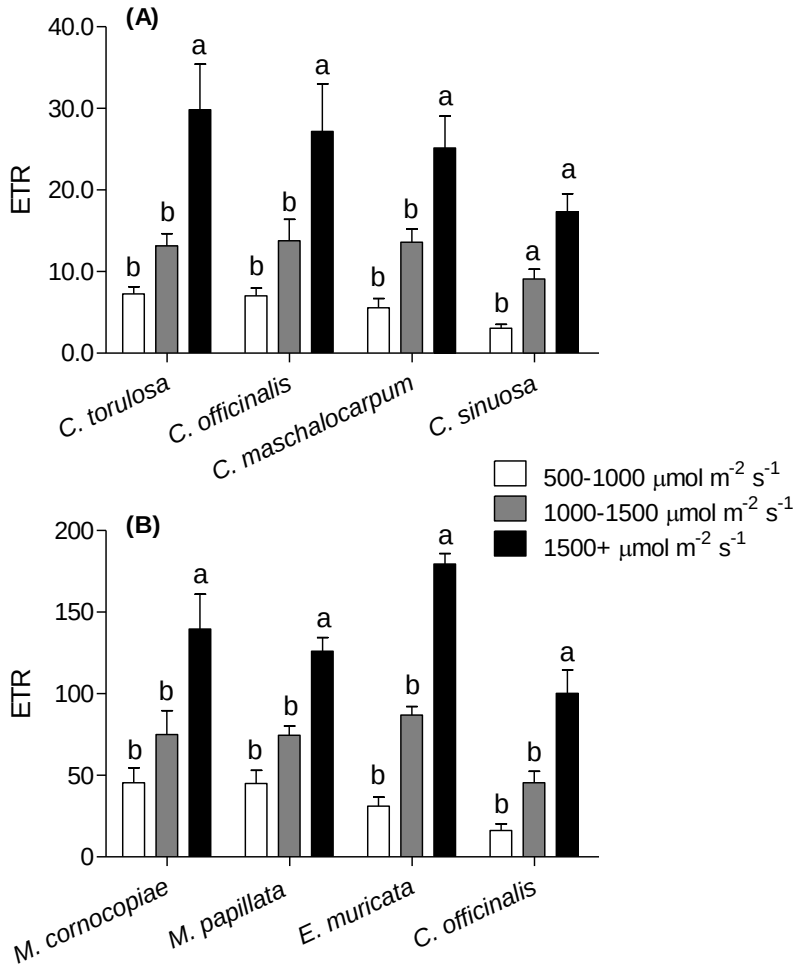

Figure 4.6. PAM fluorometry of subcanopy algae and the effects of ambient outside canopy irradiance on ETR (±SE) in New Zealand (A), and Oregon, USA (B). Significant difference between groups indicated by different letter using two-way ANOVA and Bonferroni post-hoc test.

When the electron transport rate (ETR) of same species were examined beneath and outside of canopies, there was little difference in most cases, but generally individuals inhabiting the subcanopy showed slightly higher ETR (Fig. 4.7). Two-way ANOVA showed a significant effect of species on ETR (New Zealand, $F_{2,115} = 4.4$, $p < 0.05$; Oregon, $F_{2,59} = 7.9$, $p < 0.0001$), with no effect of canopy position and no interaction effect. The only species which showed significantly higher ETR below the canopy was *C. officinali*s from Oregon (Bonferroni post-hoc test, $t = 2.8$, $p < 0.05$). In New Zealand, *C. torulosa*, *C. officinalis* and *C. maschalocarpum* all have similar ETR in the subcanopy than outside the canopy.

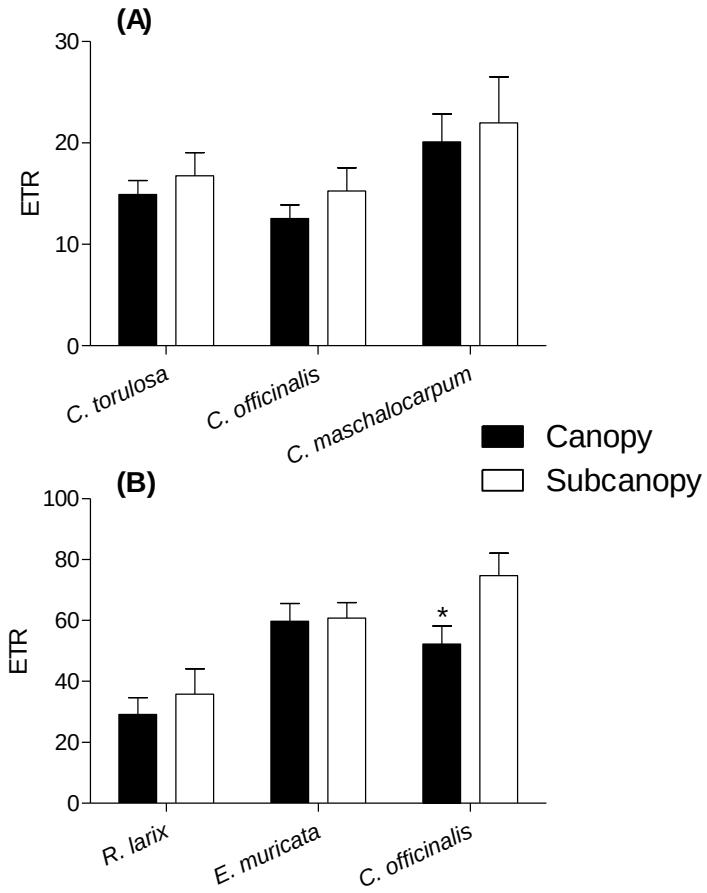

Figure 4.7. Effects of canopy shading on the relative ETR rates (±SE) of 6 species which occur beneath and outside of canopies. Species from Kaikoura, New Zealand are *C. torulosa, C. officinalis* and *C. maschalocarpum* and the species from Fogarty Creek and Bodega Bay USA are *Rhodomela larix, Endocladia muricata* and *Corallina officinalis*. Significant difference between canopy and subcanopy indicated by * (* P<0.05).

4.3.3. *Above canopy and below canopy irradiance dynamics*

There was wide variation in the amount of light energy reaching the subcanopy during hours of bright sunlight (c. 1500 µmol m^{-2} s^{-1}; Fig. 4.8). Irradiance levels in the subcanopy ranged between 50-500 µmol m^{-2} s^{-1} over periods as short as 1-2 minutes. Variation in irradiance reaching the subcanopy was most likely associated with the movement of the canopy over the sensors. The position of the sensor in association with the angle of the sun had some effect on the irradiance reaching it, but this was true mainly for the individual sensor oriented behind (in relation to the suns angle of incidence) the algal assemblage. Comparisons of above and below canopy irradiance showed that spikes in above canopy irradiance over 1000-1800 µmol m^{-2} s^{-1} were associated with spikes in

subcanopy irradiance. At low levels of ambient irradiance, all subcanopy sensor positions had very low irradiance (below 100 µmol m^{-2} s^{-1}), but during high ambient irradiance most of the subcanopy positions had a noticeable rise in irradiance with some sites reaching over 500 µmol m^{-2} s^{-1}.

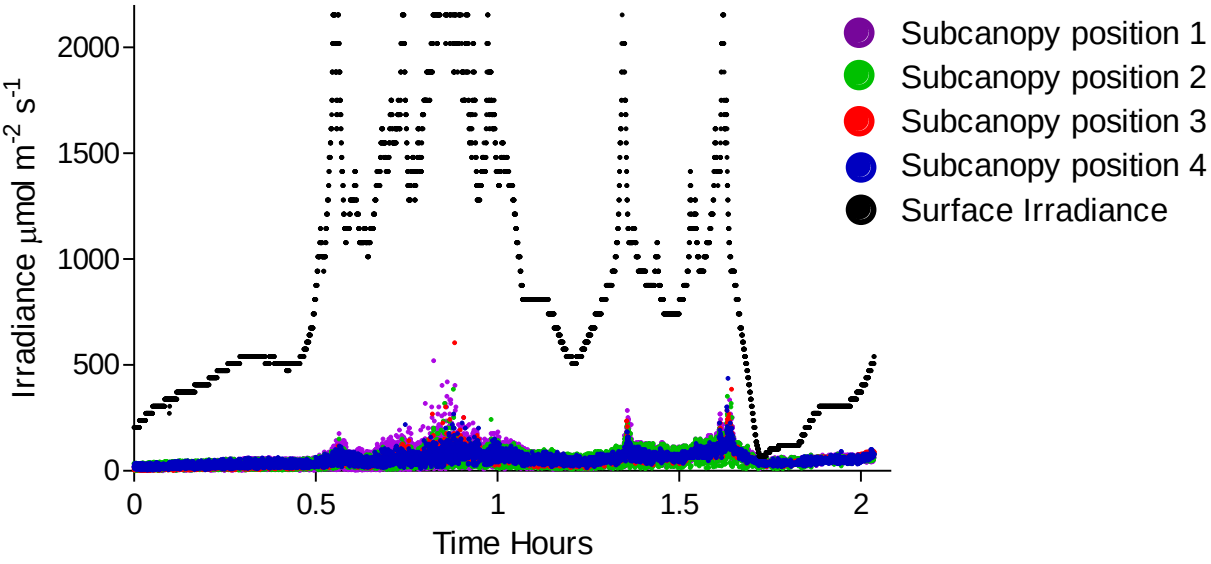

Figure 4.8. Surface and subcanopy irradiance around a *H. banksii* assemblage over a 2 hour period during summer 09. Loggers placed at four positions surrounding an assemblage dominated by *H. banksii*.

To understand the mechanisms driving the two-stage rise in production (Fig. 4.2 and Fig. 4.3), the light environment above and below the canopy was analysed (Fig. 4.9). Subcanopy irradiance was approximately 20 times lower than above-canopy irradiance. There was very little variation in irradiance beneath canopies under low ambient light conditions, but as above canopy irradiance increased so did the variability in the subcanopy irradiance. This was due to the movement of the canopy with water motion, constantly covering and exposing the subcanopy to higher levels of irradiance. Although movement of the canopy occurs regardless of light intensity, the diffuse radiation during cloudy days (i.e., low irradiance) results in decreased shading from the canopy. Interestingly, the irradiance level at which the compensation point (37.5 µmol m^{-2} s^{-1}, Table 2.1, Chapter 2) of the subcanopy assemblage was reached, occurred at around 1500 µmol m^{-2} s^{-1} surface irradiance for *H. banksii* and at approximately 1200 µmol m^{-2} s^{-1} for *C. torulosa*. Furthermore, these irradiance levels were almost identical to the levels at which the second rise in production occurs in intact assemblages

(Fig. 4.2). Linear regressions for both assemblages showed good fit; *H. banksii* r^2 = 0.60, *C. torulosa* r^2 = 0.67.

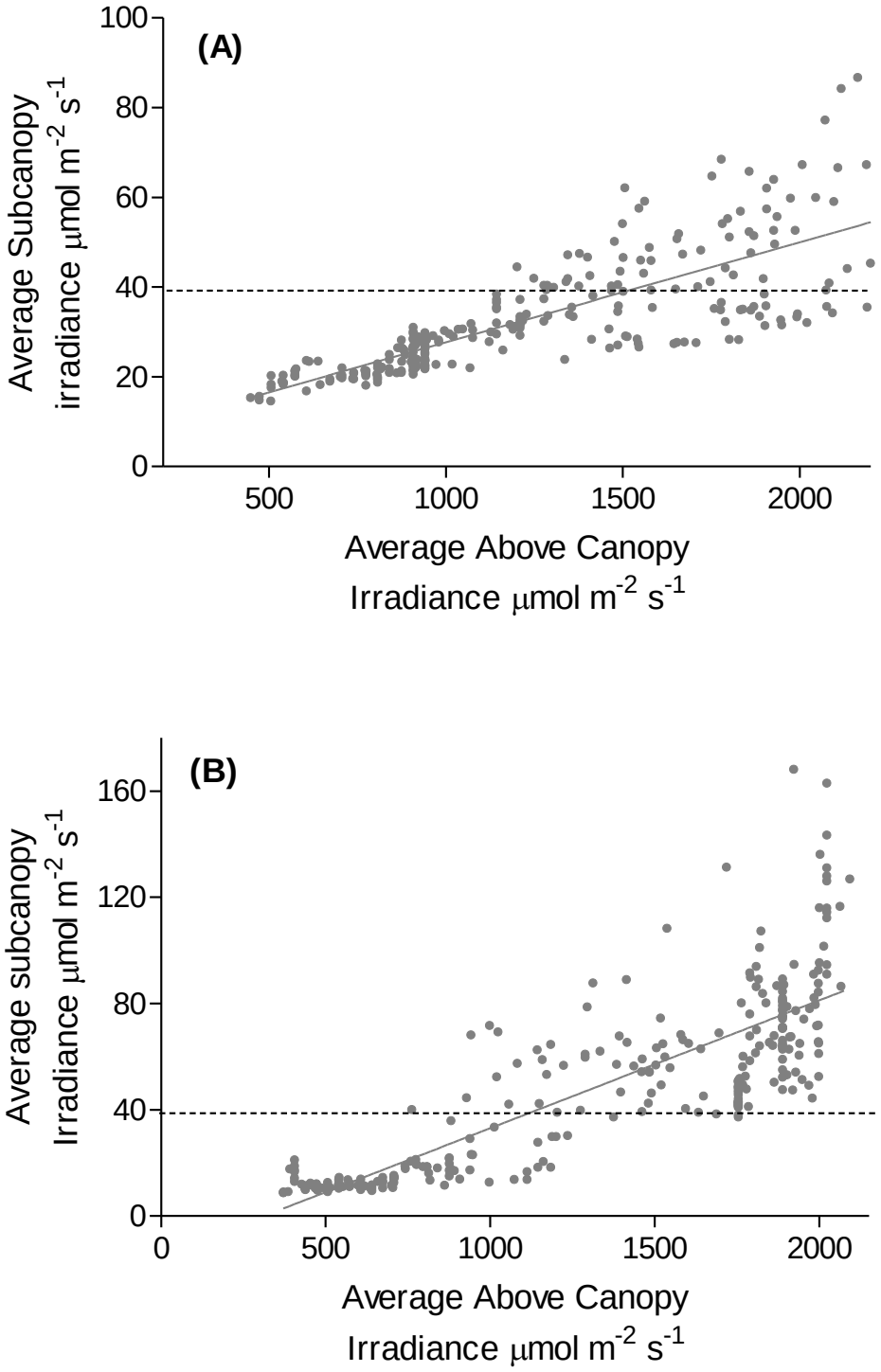

Figure 4.9. Effects of above canopy irradiance on subcanopy irradiance in assemblages dominated by *H. banksii* (A) and *C. torulosa* (B). Dotted line represents compensation point of subcanopy species (irradiance level where photosynthesis and respiration are equal).

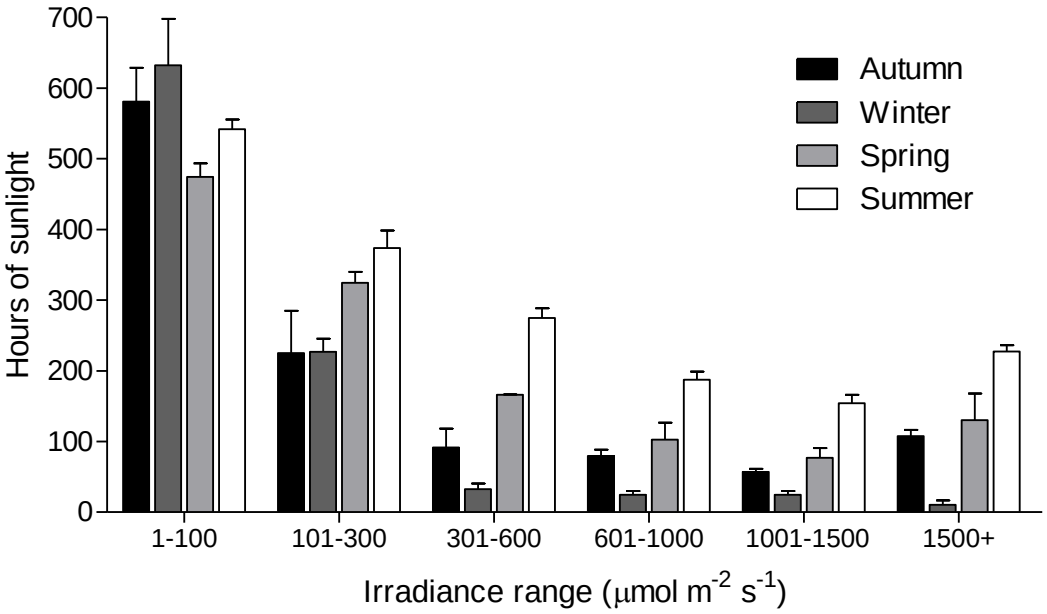

Figure 4.10. Frequency of irradiance values on open reef occurring in several irradiance ranges and the variation between seasons. Data logged at 5 minute intervals averaged over 2 years (±SE).

The frequency distribution of irradiance values was skewed towards low levels in all seasons (Fig. 4.10). The large number of irradiance hours falling between 1-100 μmol m^{-2} s^{-1} was due to periods of sunrise and sunset, as irradiance was recorded 24 hours a day 365 days a year and represent all light recordings above 0 μmol m^{-2} s^{-1} (complete darkness). Irradiance levels above 1500 μmol m^{-2} s^{-1} were infrequent compared to irradiance below 600 μmol m^{-2} s^{-1}. Irradiance recorded over two years showed that 75% of total irradiance fell between 1-600 μmol m^{-2} s^{-1}. However, irradiance above 1000 μmol m^{-2} s^{-1} represented only 16% of total annual irradiance or 1600 hours. The number of irradiance events above 1500 μmol m^{-2} s^{-1}, although small compared to low irradiance events, still represented 1000 hours of high irradiance or 10% of total annual irradiance. This is not inconsequential and has the potential to be extremely important to overall primary production on these reefs.

4.3.4. *Algal diversity and primary production*

The number of species in an assemblage was positively related to primary production at light levels above 1500 μmol m^{-2} s^{-1} (Fig. 4.11). The number of species found in these assemblages represented natural species variation within the high-mid shore zone of Oregon and New Zealand reefs. Species diversity and identity within assemblages tested

across Wairepo/North Reef and Fogarty Creek/Yachats Reef is shown in Chapter 5 (Fig. 5.6 and 5.9). At low irradiance, the number of species was weakly related to production in New Zealand assemblages and, in general, was unrelated to production in Oregon assemblages. A neutral effect occurs because light levels were too low for species to use effectively. These trends and relationships were similar on a per-area and per-biomass basis for New Zealand assemblages, but not for Oregon assemblages. The slope of the linear regression for New Zealand assemblages was significant when standardised by reef area (r^2 = 0.46, $F_{1,59}$ = 50.62, p < 0.0001) and dry weight (r^2 = 0.23, $F_{1,59}$ = 16.78, p < 0.0001) at high irradiance. In the Oregon assemblages, production increased in a relatively linear fashion with diversity when standardised by reef area (r^2 = 0.13, $F_{1,45}$ = 5.2, p < 0.05), but when standardised by dry weight (third order polynomial, r^2 = 0.16), production increased with diversity to 7-8 species, but higher diversity lead to a decline in production.

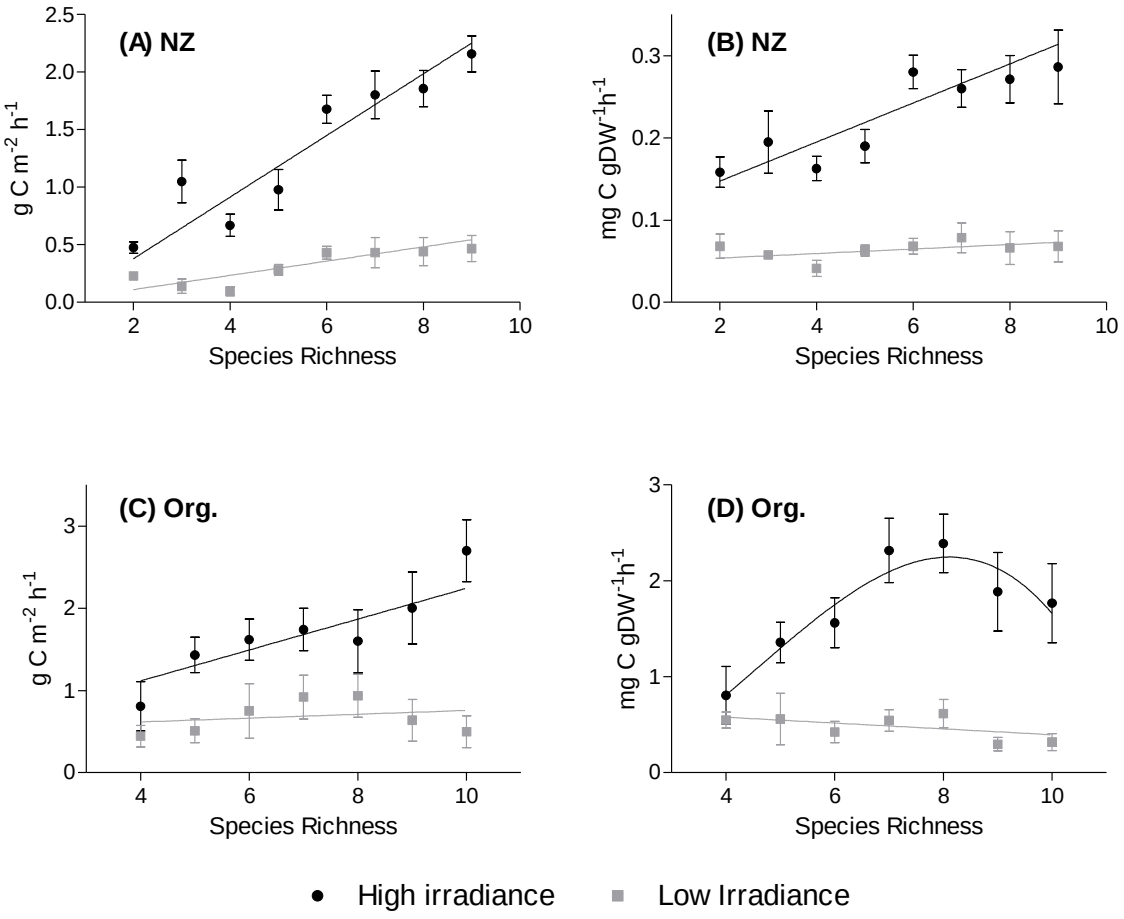

Figure 4.11. Effects of species richness on primary production (±SE) at high and low light intensity in New Zealand and USA. High irradiance between 1500-2000µmol m^{-2} s^{-1}, low irradiance between 50-350µmol m^{-2} s^{-1}. Data are standardised by reef area (g C m^{-2} h^{-1}) and dry weight (mg C gDW^{-1} h^{-1}).

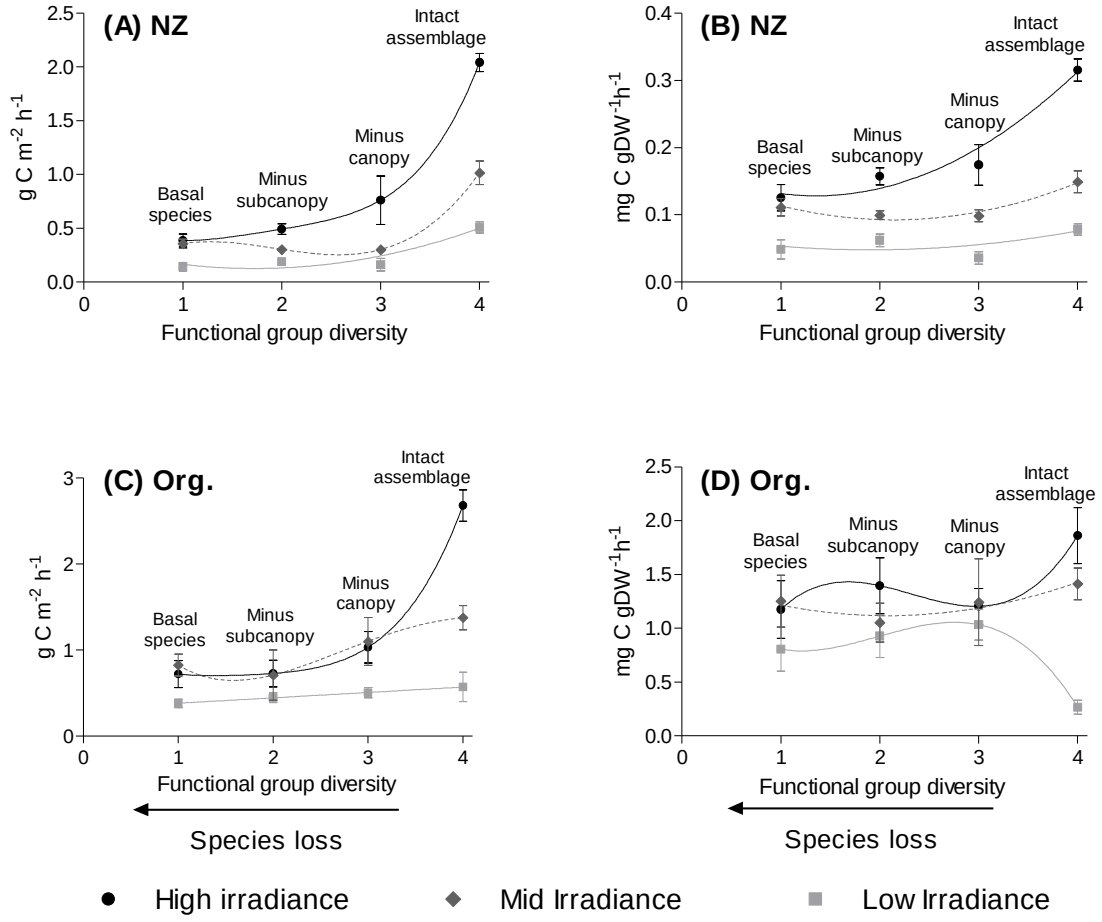

Figure 4.12. The effects of non-random species removal on primary production (±SE) of fucoid dominated assemblages in Kaikoura, New Zealand (*H. banksii* and *C. torulosa* assemblages) and Oregon, USA (*P. limitata* and *F. gardneri* assemblages). High irradiance between 1500-2000 µmol m^{-2} s^{-1}, mid irradiance between 700-1100 µmol m^{-2} s^{-1} and low irradiance between 50-350 µmol m^{-2} s^{-1}. Data are standardised by reef area (g C m^{-2} h^{-1}) and dry weight (mg C gDW^{-1} h^{-1}).

Non-random species loss showed a predictable decline in production with a cascading loss of canopy and subcanopy species (Fig. 4.12). In New Zealand assemblages (Fig. 4.12 A and B) the loss of the canopy caused a dramatic fall in primary production at high irradiance (Fig. 4.12 A, r^2 = 0.87, fourth order polynomial; Fig. 4.12 B, r^2 = 0.69, second order polynomial) and continued to fall with the loss of subcanopy fucoids, although less dramatic. At low irradiance there was little effect of community composition on production, but when standardised by reef area the production of the intact assemblage was much higher than the removal treatments (Fig. 4.12 A, r^2 = 0.59, second order polynomial; Fig. 4.12 B, r^2 = 0.19, second order polynomial). At high irradiance, Oregon assemblages (Fig. 4.12 C and D) showed the same relationship as New Zealand assemblages when standardised by reef area, but when standardised by dry

weight, the relationship was slightly different (Fig. 4.12 C, r^2 = 0.79, fourth order polynomial; Fig. 4.12 D, r^2 = 0.24, third order polynomial). When standardised by dry weight there was a less dramatic fall in production with the loss of canopy species. Also, after the loss of all fucoids, production went up slightly. Furthermore, at low irradiance the opposite relationship was seen, with production decreasing with increasing species diversity (Fig. 4.12 C, r^2 = 0.19, $F_{1,23}$ = 1.59, p > 0.05, linear regression; Fig. 4.12 D, r^2 = 0.49, third order polynomial). Two-way ANOVA of New Zealand assemblages showed a significant effect of irradiance (g C m^{-2} h^{-1}, $F_{2,89}$ = 59.2, p < 0.0001; mg C gDW^{-1} h^{-1}, $F_{1,89}$ = 72.2, p < 0.0001), diversity (g C m^{-2} h^{-1}, $F_{3,89}$ = 102, p < 0.0001; mg C gDW^{-1} h^{-1}, $F_{3,89}$ = 26.9, p < 0.0001), and a significant effect of irradiance across diversity (irradiance x diversity, g C m^{-2} h^{-1}, $F_{6,89}$ = 19, p < 0.0001; mg C gDW^{-1} h^{-1}, $F_{6,89}$ = 8.9, p < 0.0001). Oregon assemblages showed a significant effect of irradiance (g C m^{-2} h^{-1}, $F_{2,69}$ = 20, p < 0.0001; mg C gDW^{-1} h^{-1}, $F_{2,69}$ = 9.2, p < 0.0001), and diversity per reef area only (g C m^{-2} h^{-1}, $F_{3,69}$ = 19.0, p < 0.0001), and a significant interaction between irradiance and diversity (irradiance x diversity, g C m^{-2} h^{-1}, $F_{6,69}$ = 3.0, p < 0.0001; mg C gDW^{-1} h^{-1}, $F_{6,69}$ = 6.4, p < 0.05). At all sites, regardless of standardisation, there was a significant difference in production between high and low irradiance at high diversity (Table 4.6) and between high and mid irradiance in most cases at high diversity.

Table 4.6. Effects of diversity on the difference in production between high, mid and low irradiance. Table shows the results from one-way ANOVA and Bonferroni post-tests at each site New Zealand (NZ) and Oregon (Org.) standardised by reef area (m^2) and dry weight (g DW).

Difference between irradiance levels		NZ m^2		NZ gDW		Org. m^2		Org. gDW	
		p	*t*	p	*t*	p	*t*	p	*t*
High & Low	Diversity								
	1	ns	n/a	p < 0.05	3.1	ns	n/a	ns	n/a
	2	ns	n/a	p < 0.01	3.8	ns	n/a	ns	n/a
	3	p < 0.001	3.9	p < 0.001	4.8	p < 0.05	2.8	ns	n/a
	4	p < 0.001	17.3	p < 0.001	14.1	p < 0.001	10.8	p < 0.001	6.4
High & Mid	Diversity								
	1	ns	n/a	ns	n/a	ns	n/a	ns	n/a
	2	ns	n/a	ns	n/a	ns	n/a	ns	n/a
	3	p < 0.01	3.4	p < 0.05	3.1	ns	n/a	ns	n/a
	4	p < 0.001	10.9	p < 0.001	9.6	p < 0.001	5.7	ns	n/a

The combined effects of biodiversity and irradiance, illustrated in a three-dimensional plot, showed that increasing functional diversity and increasing irradiance enhances production (Fig. 4.13). Functional group diversity had a positive effect on production at high irradiance, but at low irradiance, production was enhanced at high and low functional diversity and reduced at mid functional diversity. Although irradiance had a positive influence on production at high diversity, at low diversity there was little effect of irradiance level. Factorial ANOVA indicates a significant effect of all univariate analyses (country, irradiance and diversity; Table 4.7). Furthermore, the interaction between irradiance and functional group diversity was significant and was particularly evident at high levels of both variables (i.e., functional diversity of 4 and high levels of irradiance), where the combined effects of each significantly enhanced production.

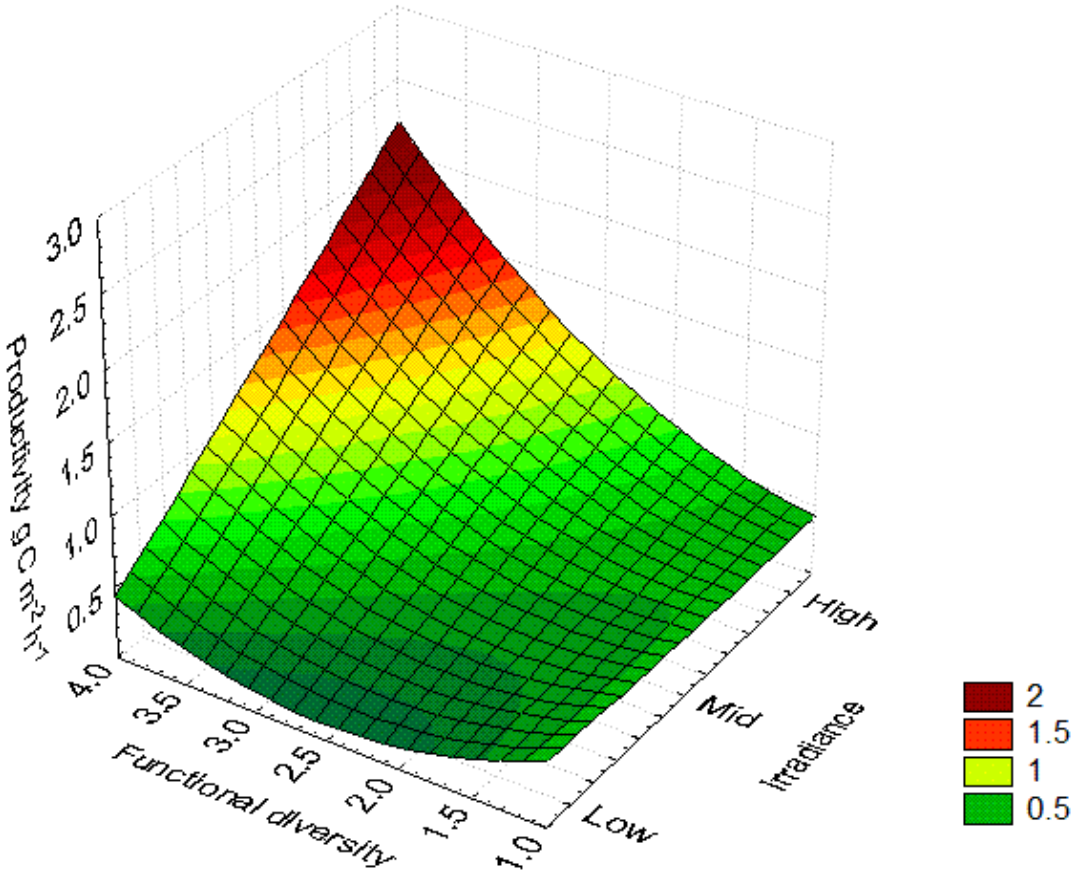

Figure 4.13. Three-dimensional plot of the effects of irradiance and functional group number on primary production (g C m^{-2} h^{-1}) in Oregon and New Zealand. Three-dimensional plane fitted using the quadratic equation (Production = 121.6+25.4*x-2.6*y+0.1*x*x-0.3*x*y+0.01*y*y).

Table 4.7. Factorial ANOVA of the effects of irradiance, country and number of functional groups on primary production in New Zealand and Oregon.

	SS	Df	MS	*F*	p
Intercept	87.7	1	87.7	730.7	<0.0001
Country	5.8	1	5.8	48.0	<0.0001
Irradiance	14.4	2	7.2	59.9	<0.0001
Diversity	26.9	3	9.0	74.6	<0.0001
Country*Irradiance	0.7	2	0.4	2.9	0.06
Country*Diversity	0.3	3	0.1	0.7	0.5
Irradiance*Diversity	14.3	6	2.4	19.8	<0.0001
Country*Irradiance*Diversity	1.2	6	0.2	1.6	0.1
Error	18.6	155	0.2		

4.3.5. *Additive partitioning of selection and complementarity*

Partitioning of selection and complementarity effects showed that at high diversity, complementarity had a significant influence on the net effect size (Fig. 4.14). In both New Zealand and Oregon assemblages the effect size was approximately one half to one third of the maximum production (mg C gDW^{-1} h^{-1}) of the assemblages tested. In New Zealand assemblages, three functional groups and above had a negative selection effect and a significant positive effect of complementarity. Two-way ANOVA of New Zealand assemblages showed a significant difference between selection and complementarity effects ($F_{2,60}$ = 33.5, p < 0.0001), and a significant effect of diversity ($F_{2,60}$ = 19.6, p < 0.0001). There was also a significant interaction between diversity and effect type (diversity x effect, $F_{4,60}$ = 7.4, p < 0.0001). Bonferroni post-hoc tests also showed significant differences between complementarity and selection effects at a functional diversity of 3 (t = 5.6, p < 0.001) and 4 (t = 5.9, p < 0.001). However, when functional diversity was two, there was no obvious difference between selection and complementarity. In Oregon assemblages there was greater variation between assemblages, but at a functional diversity of three, complementarity played a much larger role than selection. At a functional diversity of two there was no net effect of diversity on production. Two-way ANOVA of Oregon assemblages showed a significant effect of diversity ($F_{1,40}$ = 22.8, p < 0.0001), but no significant difference between effect types. However, there was a significant interaction between diversity and effect type (diversity x effect, $F_{2,40}$ = 6.8, p < 0.01). Bonferroni post-hoc tests showed a significant difference between complementarity and selection at effects at a functional diversity of 3 (t = 3.2, p < 0.01).

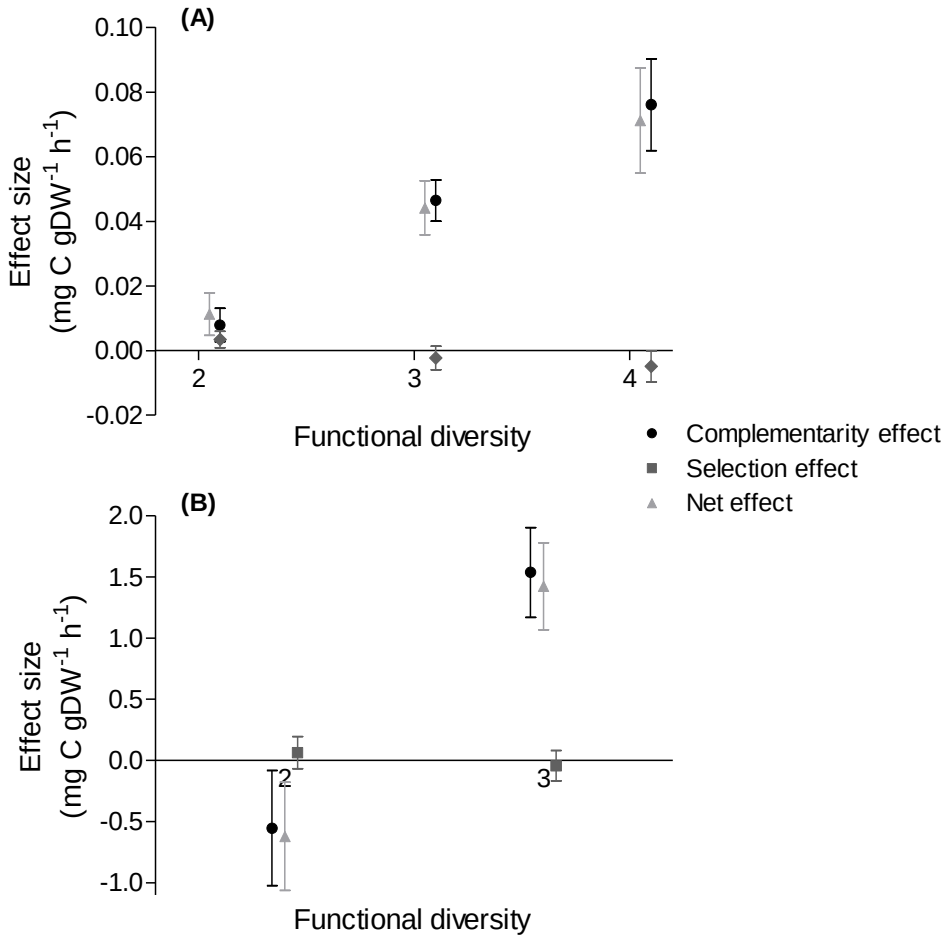

Figure 4.14. Additive partitioning of the relative effects of selection and complementarity on production (±SE). Relative contribution of complementarity and selection to production is shown as production per gram dry weight of algae in (A) New Zealand and (B) Oregon. Symbols were slightly jittered to improve visualisation.

4.4. Discussion

Primary production of macroalgae had a unique relationship with light in naturally structured, *in situ* assemblages. The two-stage rise in production at low and high irradiance occurred in all assemblages from different habitats and on different continents. These results vary from the traditional saturation curves recorded for macroalgae (Lobban et al. 1985) in that the rise at high irradiance has never been reported. Only two studies have shown a slightly linear increase in production in diverse algal assemblages, without obvious saturation of photosynthesis (Middleboe & Binzer 2004; Binzer & Middleboe 2005). They confirmed that production in aquatic assemblages is enhanced by vertical

orientation of algal thalli. Although similar relationships in terrestrial ecosystems are theorised, direct measurement of such processes are difficult, because the sheer size of assemblages makes parsing components difficult and whole-canopy production is generally determined through complex models (Williams et al. 1997). Although determination of the relative contribution of various components is possible (Mission et al. 2007), the models do not necessarily show the mechanisms involved. The research from my study suggests fundamental differences in light use between single species and assemblages. Also, this implies that natural assemblages with vertical three-dimensional structuring are able to efficiently convert incoming photons into photosynthetic production. Maximum community production is obtained when all photons are absorbed evenly among photosynthetic elements (Binzer & Sand-Jensen 2002b), which in these intertidal macroalgal assemblages occurs above 1500 μmol m^{-2} s^{-1}. The potential mechanisms for this include both how light is delivered through marine canopies and the ability of plants from different canopy levels to use light.

Manipulations showed that at high irradiance all major functional groups of *Hormosira banksii* assemblages contribute to total assemblage production. However, at low irradiance the basal species contribute very little to overall assemblage production. At low light levels, it is clear that the canopy species alone are responsible for the bulk of the production. As light levels go beyond 1500 μmol m^{-2} s^{-1}, however, understory light levels exceed compensation points for the subcanopy species and they begin to contribute to overall primary production. At higher irradiance levels the dominant subcanopy species *Cystophora torulosa* and basal *Corallina officinalis* had a significant effect on primary production, but a myriad of less dominant subcanopy species such as, *Champia novae-zealandiae*, *Colpomenia sinuosa*, *Carpophyllum maschalocarpum* and *Lophothamnion hirtum* may also enhanced production. The contributing components of Oregon assemblages were less clear, as the main production occurred in the dense canopy of *Fucus gardneri*. When standardised by dry weight, the loss of the canopy actually had a positive effect on production at low irradiance. The presence of several very productive, but low biomass, opportunistic subcanopy algae such as *Porphyra spp*, *Cladophora columbiana* and *Ulva spp* were the most likely explanation for this rise. However, the removal of basal species from the assemblage caused a fall in production suggesting that similar mechanisms caused the second rise in production in New Zealand and Oregon assemblages. The removal of subcanopy and basal species was associated with a

significant decline in production in New Zealand (regardless of standardisation) and Oregon (when standardised by reef area), indicating a role of the understory in enhancing primary production at high irradiance.

Current evidence indicates that at higher levels of irradiance (above 1000 μmol m^{-2} s^{-1}), the lower tissue levels of macroalgal monocultures receive increasing amounts of radiation, despite the relatively homogeneous structure of single species stands (Binzer & Sand-Jensen 2002a; Binzer & Sand-Jensen 2002b; Middleboe & Binzer 2004). In terrestrial forest canopies, lower canopy levels have a higher leaf area index, which enhances the efficiency of light capture (Stenberg et al. 1998), but monospecific stands of algae do not behave like this due to the changing orientation of thalli (caused by waves and currents; Binzer & Sand-Jensen 2002b). Unlike monocultures of algae, the assemblages tested in this study were comprised of multiple species with various thallus morphologies, making the lower canopy levels more efficient at capturing irradiance. This may have resulted in a much higher efficiency of light uptake than observed in the simple monospecific macroalgal stands as used by Binzer & Sand-Jensen (2002a & b).

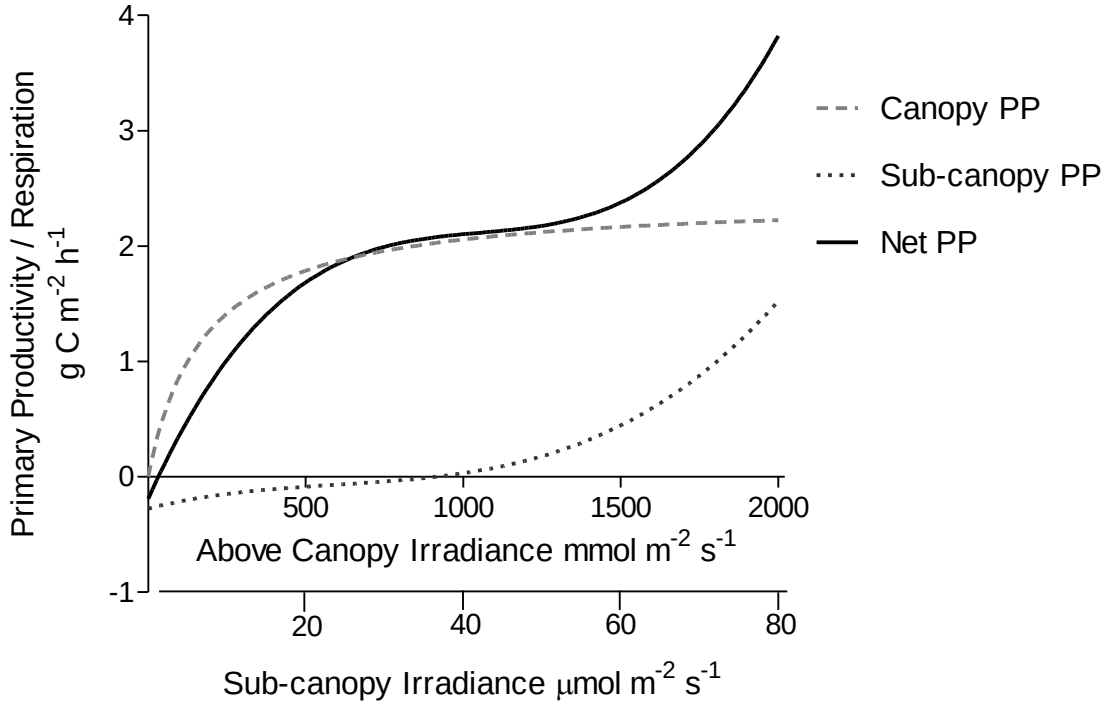

Figure 4.15. Model of primary production *in situ* and the components of the assemblage responsible for inflection points. Graph shows the above canopy irradiance and the relative subcanopy irradiance and its effects on primary production of the various community components.

The role of the subcanopy in assemblage production is corroborated by evidence of irradiance levels reaching the understory. According to the compensation point of the basal assemblage (Chapter 2), net production occurs after 40 μmol m^{-2} s^{-1}. Interestingly, subcanopy irradiance reached 40 μmol m^{-2} s^{-1}, when ambient irradiance reached 1500 μmol m^{-2} s^{-1}, the same irradiance levels at which the second rise in assemblage production occurs (Fig. 4.15). The large variation in subcanopy irradiance at high ambient light levels shows the role of canopy movement on subcanopy irradiance. At low ambient irradiance variation in subcanopy irradiance was very low, indicating the difference between diffuse and beam radiation. Studies on terrestrial forest ecosystems suggest that during days of diffuse radiation, production may in fact be higher due to the decreased volume of shade within a forest canopy (Roderick et al. 2001). There is no evidence that this occurs in marine macroalgal assemblages, which appear to be much more productive during high light levels. A major contrast between terrestrial and marine ecosystems, however, is in the movement of canopy species and how light is delivered to areas below. The swaying of tress in the wind and the great height of canopies relative to subcanopy species will generally be far different from intertidal algal assemblages where the canopies are short in height and move about significantly, even in calm sea conditions. Furthermore, evidence suggests that stipitate fucoid algae such as *Durvillaea antarctica* may be less rigid than their laminarian counterparts such as *Laminaria hyperborea*, making them more compliant to wave motion (Harder et al. 2006). This has interesting implications for the delivery of light to the subcanopy, with the more flexible fucoid species potentially offering more variation in irradiance to the subcanopy than similar laminarian species. For example, measurement of the subcanopy light environment beneath the rigid canopy of *Postelsia palmaeformis* indicates a fast decline in subcanopy irradiance and that light flecks from canopy movement do not make a measurable contribution to understory irradiance (Holbrook et al. 1991). Canopies dominated by flexible fucoid algae may have very different properties compared to other photoautotrophic assemblages, and canopy movement may be vitally important to the light delivery to subcanopy algae in these systems.

The ability of these subcanopy species to use short bursts of irradiance has significant implications for how production in marine assemblages is viewed. The delivery of light 'flecks' is an important process in the production of subcanopy plants in tropical forest ecosystems (Pearcy 1988; Chazdon & Pearcy 1991; Kursar & Coley 1993;

Valladares et al. 1997), and a similar process may be important in marine macroalgal assemblages. Light flecks have been shown to contribute up to 80% of the total light flux to the understory of tropical rainforests (Kursar & Coley 1993). Evidence shows that several fucoid and laminarian species are able to use fluctuating light effectively (Dromgoole 1987). Likewise, PAM fluorometry is based on the measurement of chlorophyll fluorescence from bursts of light approximately 1 second long (Schreiber 2004), showing the ability of algae to use light flecks. Furthermore, increasing frequency of light fluctuations is associated with the enhancement of photosynthesis, possibly due to post-illumination bursts of CO_2 (Dromgoole 1988). Variation in irradiance over periods shorter than 1 second was responsible for the highest levels of production (Dromgoole 1988), suggesting that natural variation in irradiance due to canopy movement could, in fact, be enhancing the steady state photosynthesis of subcanopy algae. Furthermore, the dominant period of ocean swells is typically within the 5-20 second range, and light flashes of this intensity have been shown to significantly increase light use efficiency in certain macroalgae (Wing et al. 1993). The delivery of light flecks to the understory during canopy movement may prove to be an important process in overall assemblage production. This has implications for the mechanisms underpinning the role of biodiversity on ecosystem function in autotrophic communities, particularly in regards to light delivery and resource partitioning.

Recent ecological literature has shown that species diversity generally enhances ecosystem function (Duffy 2009). This study is in agreement with this relationship, with increasing algal diversity enhancing primary production. Furthermore, the role of diversity is also dependent upon irradiance, with diversity only enhancing production at high irradiance. As well as natural variation in species diversity, the effects of non-random species loss were tested. There have been many calls for studies to test the effects of non-random species loss on various forms of ecosystem function (Stachowicz et al. 2007; Bracken et al. 2008). Non-random species loss has a dramatic effect on the primary production of these assemblages. Typically in these intertidal fucoid assemblages the canopy is the first species lost, followed by a subsequent burn-off of the subcanopy species, leaving predominantly turf forming algae (Lilley & Schiel 2006). The effects of this trajectory of species loss on primary production reveals a large drop in function within these assemblages. Canopy forming algae provide essential services by facilitation in the intertidal environment (Bertness et al. 1999; Lilley & Schiel 2006), but are also

essential to the primary production of these communities. Once the canopy species are lost there is a cascading effect on community composition and, therefore, on production. The effects of non-random species loss show that regardless of the unit of standardisation and the continent, canopy loss causes a dramatic fall in production. Furthermore, this relationship is observed only at high irradiance, whereas at low irradiance, functional diversity has very little impact on primary production.

It appears that at high irradiance there is some form of complementarity occurring, but at low irradiance there is significant competition for light. Evidence suggests that heterogeneity of resource distribution may enhance the effects of biodiversity on ecosystem function (Tylianakis et al. 2008). The heterogeneity of light delivery to canopy and understory macroalgae has the potential to be equally important to the biodiversity-function relationship in marine macroalgal assemblages. Furthermore, it appears that resource levels, as well as resource distribution have a particularly large effect on the relationship between diversity and production. Experiments testing the effects of diversity on production at different levels of nutrient enrichment show that enriched treatments elicit a stronger positive effect of diversity on production (Reich et al. 2001; Fridley 2002). The lack of an increase in production (and decline in production in Oregon assemblages) with diversity at low irradiance suggests a high level of inter-species competition for light (Fig. 4.11, Fig. 4.12 and Fig. 4.13). At high irradiance, however, increasing diversity enhances overall assemblage production. The switch from competition to complementarity with irradiance suggests a complex relationship between canopy and subcanopy species (Fig. 4.16). Without sufficient testing at various irradiance levels, these canopy and subcanopy interactions may be interpreted as competitive, and the role of complementarity may be missed.

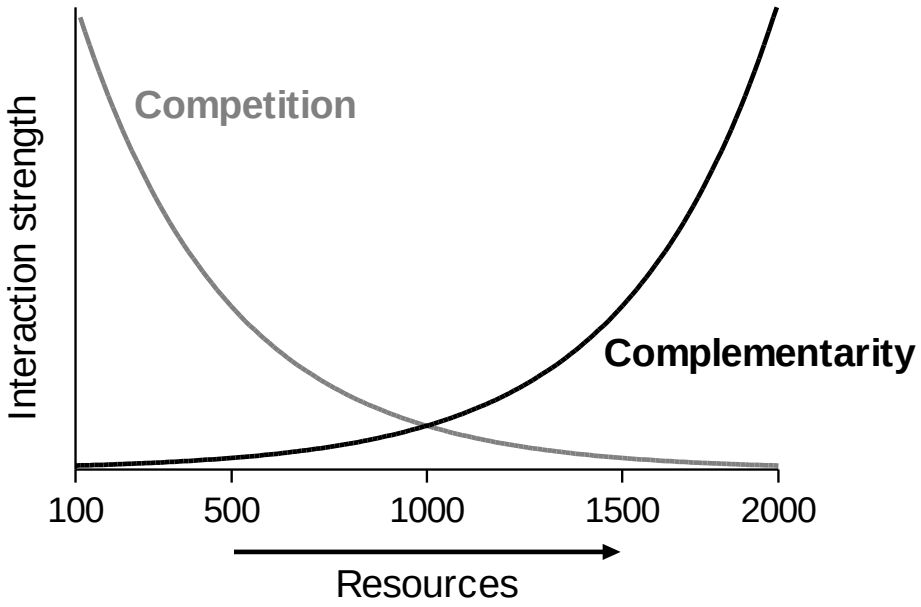

Figure 4.16. Schematic representation showing the effects of resource levels on the interaction strength of competition and complementarity.

Enhancement of ecosystem function, in this case primary production, is theorised to occur due to complementarity of resource use, or selection effects (Hector 1998; Loreau 1998; Loreau & Hector 2001). A number of studies have now established that selection effects are insufficient to fully explain enhanced production with species diversity and that some form of complementarity is involved in the enhancement of ecosystem function (Loreau & Hector 2001). The complementarity hypothesis states that because of niche differences among species, individuals in a mixture experience, on average, less niche overlap in resource use than corresponding monocultures. Complementary light use has been suggested as one possible mechanism yielding positive effects of species diversity (Naeem et al. 1994), but few studies have attempted to explore this. Although appealing, this hypothesis has little empirical evidence (Yachi & Loreau 2007). Recently the contribution of complementary light use was tested in grassland ecosystems, but indicated that mixtures rarely outcompeted monocultures (Vojtech et al. 2008). Terrestrial ecosystems are further complicated by the partitioning of above- and below-ground resources, making it difficult to draw conclusions about any one process in enhancing ecosystem function. Although Vojtech et al. (2008) show no obvious complementary light use, other studies show complementary below-ground nutrient use (Fridley 2002). The structure of grassland ecosystems may not be predisposed to complementary light use, with assemblages typically being very compact, with no

obvious differentiation in canopy layers. Marine macroalgal assemblages, however, do have obvious differentiation in canopy layers, and are generally more open and less dense. The effects of density on plant survival suggests that there are inherent differences between marine algae and terrestrial plants (Schiel & Choat 1980). Contrary to terrestrial plants, density had a positive effect on the survival of monospecific stands of algae (Schiel & Choat 1980). Although this is not true of all marine algae (Reed 1990), such a relationship may be more common in intertidal and shallow subtidal fucoid algae which are exposed to strong wave forces and are generally less rigid than many laminarian species (Harder et al. 2006). The results from my study suggest that even in dense macroalgal assemblages light is distributed amongst thalli, particularly at high irradiance. The high energy of the marine environment and the flexibility of macroalgae may allow light to reach most plants, in even the most crowded assemblages.

My study indicates that even in dense macroalgal assemblages subcanopy species are able to make use of the limited light resource. Furthermore, when the effects of complementarity and selection are partitioned using methods described by Loreau & Hector (2001), complementarity is significantly more important at high functional diversity, with selection negative in most cases. Evidence from my research indicates that complementary light use can occur under the right circumstances, and unlike terrestrial ecosystems foregoes any complication caused by differences in belowground resource use. Although there are fundamental differences between marine and terrestrial ecosystems, this research gives evidence for the potential role of complementary light use in enhancing primary production of multi-species assemblages. Furthermore, the important role of short bursts of high irradiance, analogous to sun-flecks observed in forest ecosystems, suggests that these findings may be general to layered autotrophic assemblages. Marine macroalgal assemblages may provide considerable insight into the light use in autotrophic assemblages which is difficult or impossible to achieve in many terrestrial ecosystems on a whole assemblage level due to size and the complication of partitioning above- ground and below- ground resource use.

Disturbance and primary production

Impacts of canopy and subcanopy loss on production: functional roles and the potential for functional redundancies

5.1. Introduction

Disturbance is a fundamental process affecting biological communities, and plays an important role in species turnover and community composition within marine systems. On a local scale, disturbance may be the most important mechanism in structuring marine communities (Menge et al. 1999; Menge 2000). Physical and biological disturbances drive temporal and spatial heterogeneity in ecosystems and directly affect the evolution of natural histories (Sousa 1984). Shallow marine ecosystems are extremely dynamic and are affected by a range of disturbances including, wave disturbance, emersion and desiccation, salinity changes, sedimentation, as well as biotic disturbances such as predation. Changing disturbance regimes, often due to human activities, are potentially altering the composition and structure of biological communities. Furthermore, increasing disturbance from species removal and invasions (Jackson et al. 2001) and the pervasive threat of global warming (Walther et al. 2002) are having substantial impacts on both marine and terrestrial ecosystems. Therefore, understanding how disturbance, anthropogenic or otherwise, affects biological communities will give insight into how best to mediate the potential effects of human disturbance.

Because shallow, temperate, rocky reefs are dominated by macroalgae, which are vulnerable to a wide range of disturbances, e.g., pedestrian disturbance (Keough & Quinn 1998; Schiel & Taylor 1999), selective removal of species (Kingsford et al. 1991), UVB damage (Franklin & Forster 1997) and sedimentation (Schiel et al. 2006), it is important to understand the impacts to these assemblages. Furthermore, the alteration of frequency or intensity of disturbance could have large scale impacts on the structure and functioning of these communities. Canopy forming algae are key structural elements and are often responsible for a large proportion of the intertidal diversity by ameliorating physical stress beneath the canopy (Bertness et al. 1999; Benedetti Cecchi et al. 2001; Lilley & Schiel 2006; Schiel & Lilley 2007) and loss of, or reductions in the abundance of macroalgae could have wide-reaching consequences on the associated flora and fauna. Canopy algae are thought to be in worldwide decline and many localised extinctions have been documented (Benedetti Cecchi et al. 2001; Airoldi & Beck 2007). Loss of macroalgae, the dominant primary producers of temperate intertidal reefs, may result in major reductions in carbon fixation, and could have consequences reaching beyond the intertidal environment.

Although many studies have tested the effects of partial or total canopy loss on community composition and diversity (Bertness et al. 1999; Lilley & Schiel 2006; Schiel & Lilley 2007), little has been done to test the effects of canopy and subcanopy loss on primary production and the recovery of primary production over time. Following disturbance, assemblages are subject to unique shifts in species composition due to re-colonization and succession of the site (Sousa 1984). The trajectory of re-colonization is often determined by the life histories of local species, with short-lived ephemeral species (which are often very productive) often dominating the early successional stages of disturbed patches (Chapman & Underwood 1998; Lilley & Schiel 2006). Longer lived perennial species recruit slower, but generally dominate the intertidal assemblages of Southern New Zealand (Schiel 1990). The resulting effects of disturbance on primary production could have either a negative, positive or nuetral impact on overall community production. The role of successional trajectory on primary production has received little attention and may give insight into the role of the numerous ephemeral species associated with these systems.

Although the role of canopy-forming macroalgae is generally well understood, the functional roles of the subcanopy species are often neglected. The subcanopy of terrestrial forest ecosystems has been suggested to contribute up to 30% of total ecosystem production (Mission et al 2007), and the subcanopy of macroalgal assemblages has the potential to be equally as important. Furthermore, subcanopy, and turf-forming calcareous algae play a significant role in reef ecology with have the ability to inhibit fucoid recruitment (Airoldi & Cinelli 1997; Airoldi 1998; Connell 2005) and enhance the recruitment of some laminarian species (Thompson 2004). However, the role of coralline turf in primary production is less well understood, and may be considered negligible compared to canopy-forming species, due to their relatively low rates of carbon fixation (Littler & Arnold 1982). Along with coralline turfing species, the role of numerous ephemeral algal species is poorly understood. On New Zealand reefs, a large amount of the algal diversity is ephemeral and occurs only during certain months of the year (Schiel 2006), with only a small fraction of total species diversity present at a given time. Understanding the contribution of these species to overall ecosystem production may give insight into their functional roles within intertidal ecosystems.

Understanding the functional roles of macroalgal species within intertidal assemblages will provide insight into the potential consequences of species loss on ecosysten function. One of the hypothesis predicting how ecosystems may respond to

species loss is the 'redundancy hypothesis' which suggests that the loss of a species can be compensated for by functionally similar species (Lawton 1994; Naeem et al. 2002). However, the likelihood of a redundancy scenario in nature is debated (Loreau 2004), with redundancy being incompatible with stable co-existence as predicted by classical Lotka-Volterra models of competition. Furthermore, the presence of complementarity is contrary to functional redundancy, with the two unlikely to occur simultaneously (Loreau 2004). However, functional redundancies have been reported in terrestrial systems, where the loss of a given species can be compensated for by other species with similar functional traits (Symstad et al. 1998; Symstad & Tilman 2001). The potential for redundancies in the canopy and subcanopy functional groups is vital to our understanding of the potential impacts of increasing levels of human disturbance on these reef systems.

Macroalgal primary production is vital to the functioning of these near-shore ecosystems, with carbon fixed by macroalgae underpinning the detrital food-webs of near-coastal systems. Furthermore, evidence suggests that the principle indicator of primary production in macroalgal assemblages is assemblage biomass (Reed et al. 2008). Therefore, biomass lost through disturbance has the potential to drive changes in production dynamics of these systems. Loss of biomass from various canopy levels may give an indication of the functional roles of some of the less conspicuous, subcanopy species. Understanding the effects of canopy and subcanopy loss on primary production and the subsequent effects of succession on that production may give insight into the wider community effects of disturbance. Furthermore, the potential for replacement by species with similar functional traits may give evidence for redundancy within these systems. The use of *in situ* photorespirometry provides a good tool to follow the primary production potential after canopy and subcanopy disturbance over time and measure recovery in terms of primary production. I test the null hypotheses that canopy and subcanopy disturbance have equal effects on primary production, and that canopy disturbance has the same effect down a shore-height gradient.

5.2. Methods

5.2.1. *Study sites, incubation protocol and standardisation*

Experimental work was done at several locations in New Zealand and Oregon, U.S.A. Mid shore canopy manipulation experiments on *Hormosira banksii* were done at Wairepo Reef, Kaikoura. These mid shore assemblages were dominated by the canopy forming fucoid alga *H. banksii*. The understory was dominated by the ubiquitous *Corallina officinalis*, as well as the less dominant fucoid *Cystophora torulosa*. Primary production of Northern hemisphere intertidal macroalgal assemblages was done on two reefs in Oregon (Fogarty Creek and Yachats Reef; see Chapter 1 for map). The mid shore assemblages were dominated by *Fucus gardneri* and the high-mid tidal zone was dominated by *Pelvetiopsis limitata*. The understory was dominated by myriad species including *Mastocarpus papillata*, *Mazzaella cornocopiae*, *Endocladia muricata*, *Rhodomelia larix*, *Ulva* spp and *Porphyra* spp. Primary production gradient experiments were also done at Wairepo Reef, except for experiments involving *Durvillaea antarctica* which were done at North Reef, Moeraki.

Incubations were done using the custom designed photorespirometry chambers (protocols for incubations and chamber design described in Chapter 3). These were sealed around target assemblages immediately prior to incubations and removed after incubations to limit any long term disturbance of the target assemblage (Fig. 5.1). For *H. banksii*-dominated assemblages, this allowed for the same assemblages to be sampled over time, while being exposed to natural conditions. These long term plots were marked using tags bolted into the substratum. To enable the effective sealing of the chambers around the target plots, a two compound epoxy resin was used to fill in deeper cracks within the substratum, but care was taken not to change the reef composition so much that pooling of water occurred. On flat surfaces the only manipulation of the reef was drilling the holes for the rawl plugs. Before incubations were done, all visible invertebrates were removed from the assemblages.

Figure 5.1. Chamber setup on Wairepo reef, Kaikoura, NZ. Chamber set up in the *Hormosira banksii* dominated mid-shore zone.

For analysis, primary production data were standardised by either grams dry weight of algal material (mg C gDW^{-1} h^{-1}) or by area of reef substratum (g C m^{-2} h^{-1}). Because of the long term nature of many of these experiments, the biomass of algal assemblages could not be directly measured. Therefore, an estimate of biomass was used to standardise production by grams dry weight of algal material. This was done by calculating the relationship between total percent cover of algae and dry weight. Algae were harvested from an area of reef the same size as the chamber (i.e., a diameter of 25cm) on numerous plots outside the experimental and control treatments. Before removal from the substrate, percent cover of all algae was recorded. Algae were then dried in a conventional oven for 24 hours at 50˚C and the dry weight recorded. The linear relationship between dry weight of algae and total percentage cover of algae was used to determine the dry weight biomass of algae in experimental plots that could not be harvested. In some cases where long term measurements were not required, the dry weight of algae was directly measured in the experimental plots (i.e., in all Oregon experiments, and in the shore height gradient experiments). Standardisation by reef area was done by multiplying the surface area enclosed by the chamber to a metre squared.

Figure 5.2. Base plate (top) and chamber (bottom) fixed around assemblages dominated by *Fucus gardneri* on Fogarty creek reef, Oregon, USA.

5.2.2. *Effects of canopy and subcanopy disturbance on production and community composition in mid shore assemblages*

The primary production of intertidal assemblages and the resultant effects of canopy removal were tested in fucoid-dominated communities on sheltered reefs of the Kaikoura Peninsula. To examine the effects of canopy loss on primary production, control and removal plots were set up on Wairepo Reef. Three initial treatments were used: (1) control, (2) minus the less dominant subcanopy species *Cystophora torulosa* while maintaining the cover of the dominant *H. banksii* and other subcanopy/basal species and (3) minus the dominant canopy fucoid *Hormosira banksii* leaving the subcanopy and basal assemblage intact. Also, a fourth treatment was added to test the role of subcanopy species on overall production approximately 6 months after the initiation of the first three

treatments. In this treatment the basal species *Corallina officinalis* was removed from the assemblage (along with any attached epiphytes), leaving the canopy and subcanopy species intact. The first three treatments (i.e., control, minus *C. torulosa* and minus *H. banksii*) were set up in 2008 and the fourth treatment (minus *C. officinalis*) was added in 2009. Treatment plots were set up by removing the canopy or subcanopy species over a 50 x 50 cm area, within which the chamber was set up. Three replicates of each treatment were used.

For each treatment and replicate, data were collected under a variety of irradiance regimes from high (full sunlight) to low irradiance (extensive cloud cover). For this reason, data on a single replicate assemblage was often collected over several days, and an entire sampling run (i.e., all replicates of all treatments) was collected over several weeks. The three main treatments were analysed directly after species removal (time 0), 3 months, 6 months, 1 year, and 2 years after removal. Furthermore, data were collected during all seasons to gain an understanding of intra-annual differences in primary production. The subcanopy removal treatment was tested 1 week after removal, and 6 months after removal.

To gain an understanding of the change in species composition, the recovery and succession of experimental and control plots were analysed throughout the experiment. During primary production sampling, all macroalgal species within the experimental plots were recorded and their percentage cover estimated. Macroalgal species were only recorded if they were attached and covered an area equal to or greater than 0.5% of the surface.

Table 5.1. Experimental treatments, canopy position, date that experiment started and the sampling periods after the start of the experiment.

Treatment	Canopy position	Experiment set-up date	Sampling time after start (months)	No of Replicates
Control	-	Nov-07	0, 3, 6, 12, 24	3
Minus *Cystophora torulosa*	Subcanopy	Nov-07	0, 3, 6, 12, 25	3
Minus *Hormosira banksii*	Canopy	Nov-07	0, 3, 6, 12, 26	3
Minus *Corallina officinalis*	Basal	Mar-08	0, 6	3

Comparable experiments were also done on the mid shore zone of North American rocky reefs. Assemblages dominated by two fucoid species, *Fucus gardneri* (Fig. 5.2) and *Pelvetiopsis limitata* were analysed at two sites in Oregon, USA, Fogarty Creek and Yachats Reef. However, unlike the experiments done in New Zealand, these

assemblages were sampled on a one-off visit, meaning that the trajectory of recovery could not be followed. Furthermore, in the *P. limitata* assemblages, there is only two assemblage components, the *P. limitata* canopy and the basal species (predominantly *M. papillatus* and *E. muricata*), whereas *F. gardneri* assemblages have three components, *F. gardneri* canopy, subcanopy *P. limitata*, and the remaining basal species predominantly *M. cornocopiae* and *M. papillatus*. Assemblages were sampled directly after species removal. Only 2 replicates were completed on assemblages (*F. gardneri* and *P. limitata*) minus basal species due to time constraints.

Table 5.2. Experimental treatments, the canopy position of the removed component and the date of experiment.

Dominant species	Treatment	Canopy position	Experiment date	No of Replicates (per site)
Fucus gardneri	Control	-	Jun-09	3
	Minus *Pelvetiopsis limitata*	Subcanopy	Jun-09	3
	Minus *Fucus gardneri*	Canopy	Jun-09	3
	Minus basal species	Basal	Jun-09	2
Pelvetiopsis limitata	Control	-	Jun-09	3
	Minus *Pelvetiopsis limitata*	Canopy	Jun-09	3
	Minus basal species	Basal	Jun-09	2

5.2.3. *Pathway analysis on the effects of canopy removal on mid shore assemblages*

To understand the sequence of events affecting macroalgal assemblage composition and hence primary production, a pathway analysis was performed on the *H. banksii* dominated mid shore assemblages. The pathway analysis included the canopy treatment, the effects of canopy removal on temperature and community structure, and the impacts of these factors on primary production. Pathway analysis was done using Amos v. 18.0 (Amos Development Corporation). Canopy treatment was a fixed variable with only two levels, canopy present and canopy absent. Temperature was determined by HOBO temperatures loggers placed within 3 minus canopy removal plots and 3 canopy control plots treatments, and averaged across 2 months (during December-February 2009-2010). Community composition was determined as a change in community composition over 1 year, from spring 2008 to spring 2009. This was done by plotting community composition on a PCA plot (using PRIMER software) and calculating the change in community structure as a vector. Primary production at irradiance levels above 1500

µmol m^{-2} s^{-1} (mg C gDW^{-1} h^{-1}) was used as the response variable. Analysis in Amos was done by testing the effect of one factor on another. This was calculated as a regression weight and was then divided by the estimate of the standard error, giving the critical ratio and a significance value (p-value). Furthermore, the effects of external variables, otherwise known as latent variables (E1, E2 and E3) on each factor were determined by the model.

5.2.4. *Primary production and the impacts of canopy loss across a shore-height gradient*

The relative production of macroalgal assemblages, which occur at various shore-heights, were examined to test the effects of physical stress on primary production. The corresponding assemblages at each shore height were, *Porphyra spp* high-mid shore, *H. banksii* dominated mid shore, co-dominance of *H. banksii* and *C. torulosa* low-mid shore, *C. torulosa* dominant low shore and *D. antarctica* which occurs on the fringe between immediate subtidal and low shore. *D. antarctica* incubations were only done at North Reef Moeraki, whereas *P. columbina*, co-dominant *H. banksii* and *C. torulosa*, and *C. torulosa* assemblage incubations were done at Wairepo Reef, Kaikoura (Table 5.3).

Primary production down a shore-height gradient was also tested on fucoid and laminarian species from Oregon reefs. The assemblages tested were dominated by *P. limitata* in the high-mid shore, *F. gardneri* in the mid shore and *Hedophyllum setchell* in the low shore. Primary production of *H. setchell* was only measured at the Fogarty Creek site due to tide constraints and only in 2 replicates due to tide limitations (compared to 6 replicates at two sites for *P. limitata* and *F. gardneri*). Maximum primary production of these assemblages was used to analyse the differences across the shore-height gradient.

Table 5.3. Shore-height and the dominant canopy forming macroalgal species in New Zealand and Oregon reefs.

	Dominant species	
Shore-height	New Zealand	Oregon
High-mid shore	*Porphyra spp*	*Pelvetiopsis limitata*
Mid shore	*Hormosira banksii*	*Fucus gardneri*
Low-mid shore	*H. banksii & C. torulosa*	-
Low shore	*Cystophora torulosa*	*Hedophyllum setchell*
Inter-, Sub- tidal fringe	*Durvillaea antarctica*	-

The effects of canopy removal was tested across a shore height gradient on Wairepo reef, Kaikoura. The mid shore zone at Wairepo reef is dominated by *H. banksii*, but in the low-mid zone, it changes to a co-dominance of *H. banksii* and *C. torulosa*, and in the low shore, assemblages are dominated by *C. torulosa*. The low-mid shore zone has a more diverse understory than the mid shore, and in particular, has high abundance of *Champia novae-zealandiae*. The understory of the low shore, like the mid and low-mid shore, had a high cover of *C. officinalis*, but had relatively high cover of *C. novae-zealandiae*, *Lophothamnion hirtum*, and *Halopteris virgata*. Data for canopy removal of the *H. banksii*-dominated mid shore assemblages was taken from the experiment described above (5.2.2), including the removal treatments, minus *C. torulosa* and minus *H. banksii*. The equivalent removal treatments were also done in the low-mid and low shore. The only difference was the changing dominance of the two fucoid species and their associated understory assemblages. Three replicates of each treatment at each shore height were tested.

5.3. Results

5.3.1. *Species cover and biomass*

Over two years of sampling at 9 mid shore plots (control and treatments) there was a total of 23 macroalgal species found (Fig. 5.3). The average percentage cover over the two years shows very few highly abundant species and many rare species. Rare macroalgal species generally fell into two categories, rare over time, or spatially rare (e.g., ephemeral species). The persistently dominant species were *Hormosira banksii*, *Corallina officinalis* turf, encrusting coralline and *Cystophora torulosa*. There was little variation in percentage cover of the three most dominant species over time (Fig. 5.4). Percentage cover over time in control plots indicates very consistent cover of *H. banksii*, but a slight decrease in the cover of *C. torulosa* and a slight increase in the cover of *C. officinalis*. This may be the result of seasonal differences within the experiment or a general shift in species composition within the plots.

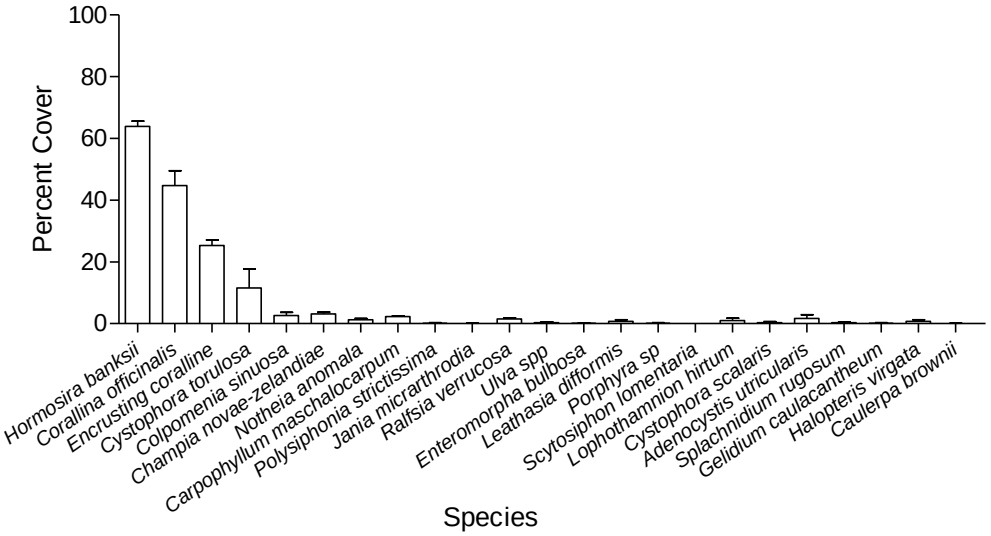

Figure 5.3. Total number of macroalgal species and average percentage cover (±SE) of macroalgal species found in experimental and control plots at Wairepo reef. Data show averaged percentage cover of macroalgae collected over 2 years of sampling at all plots.

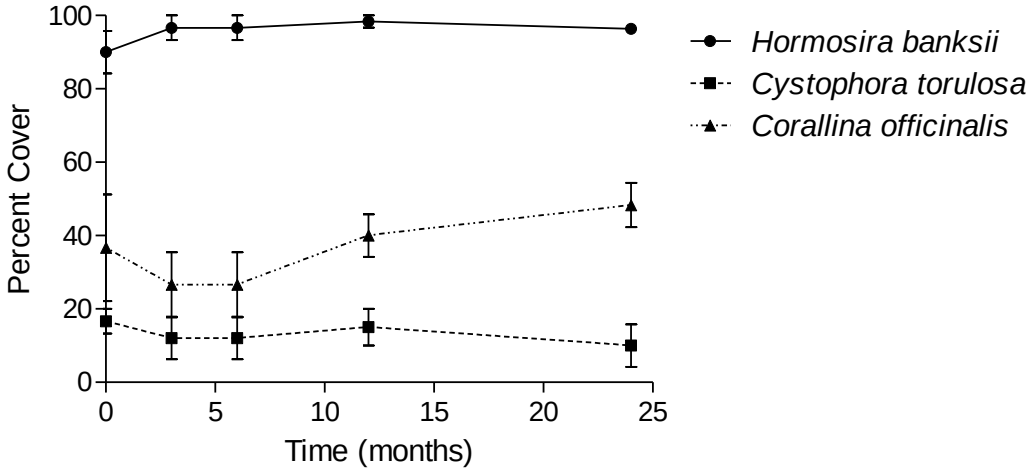

Figure 5.4. Variation in percentage cover (±SE) of the three most abundant species *Hormosira banksii*, *Cystophora torulosa* and *Corallina officinalis* over time in control plots.

The relative biomass of mid shore assemblages, like the percentage cover data, show that *H. banksii* contributes the most biomass to the assemblage (Fig. 5.5). Because experimental plots could not be harvested for biomass measurements, the species composition is slightly different from percentage cover data (Fig. 5.3). Although *C. officinalis* and *C. torulosa* contributed a significant amount of the algal cover, they

contribute one-tenth of the biomass compared to *H. banksii*. The biomass of all the other species contribute less than one-hundredth compared to *H. banksii*. The canopy-forming fucoid made up both the highest percent cover and the highest biomass of mid shore assemblages.

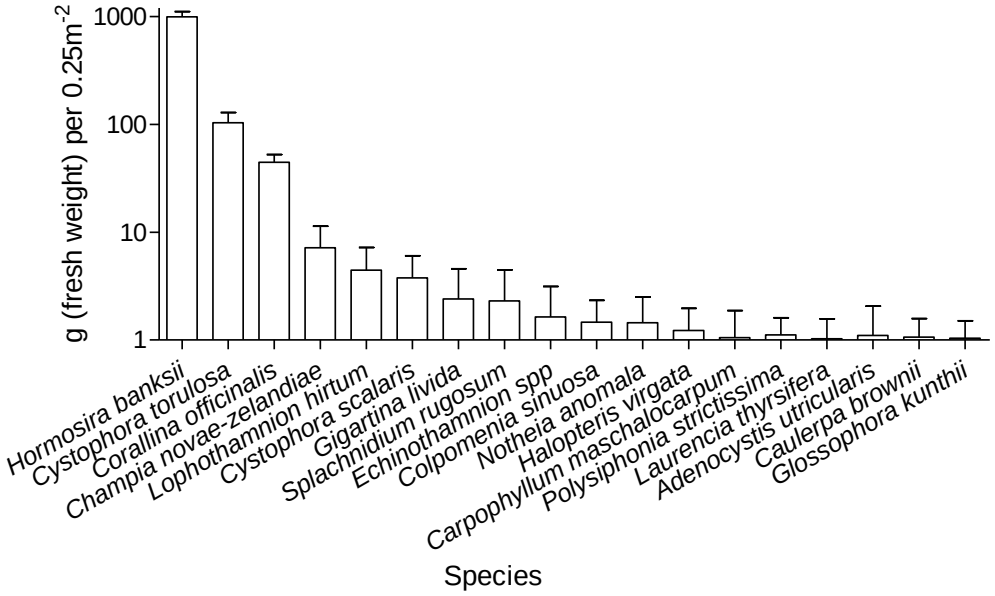

Figure 5.5. Average biomass (±SE; fresh weight per 0.25m^2) of macroalgal species from Wairepo reef, Kaikoura in the mid shore zone. Y-axis shown as a log scale.

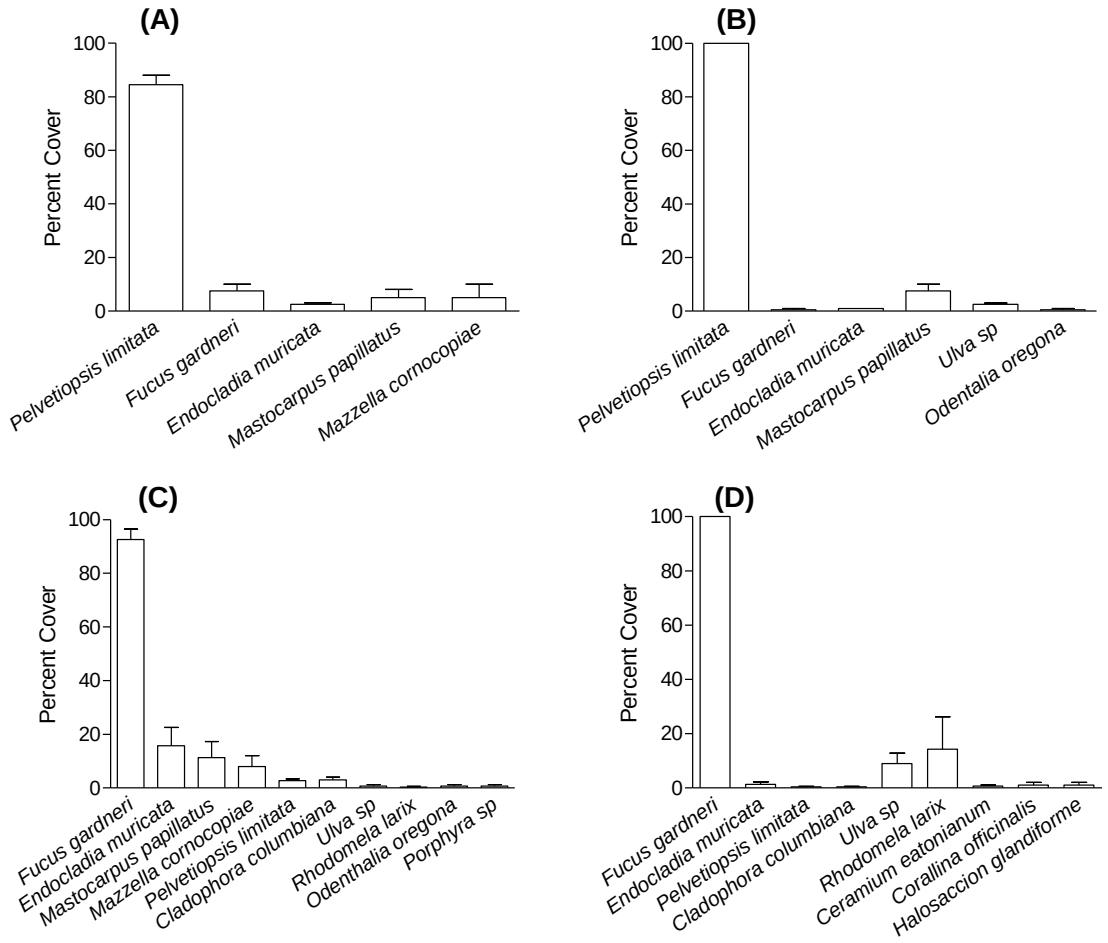

Figure 5.6. Algal species diversity and percent cover (±SE) in mid shore and high-mid shore macroalgal assemblages at two Oregon sites. Graphs show the diversity and cover of the high-mid shore *Pelvetiopsis limitata* at Fogarty Creek (A) and Yachats reef (B), as well as, the mid shore *Fucus gardneri* at Fogarty Creek (C) and Yachats reef (D).

The high-mid zone of both Oregon sites was almost completely dominated by *Pelvetiopsis limitata* with only trace amounts of a few subcanopy species (Fig. 5.6 A and B). In total, seven species were found across 6 plots (3 at each site), with no species, besides *P. limitata*, exceeding a cover greater than 10%. The mid shore of both Oregon reefs were dominated by *Fucus gardneri*, with lower abundances of many other species (Fig. 5.6 C and D). Beneath the canopy of *F. gardneri*, thirteen species were found across two sites, with several species showing relatively high cover beneath the canopy. Biomass generally followed the same trend as species cover data, with fucoids contributing a large proportion of total biomass in assemblages dominated by *P. limitata* (Fig. 5.7 A and B) and *F. gardneri* (Fig. 5.7 C and D).

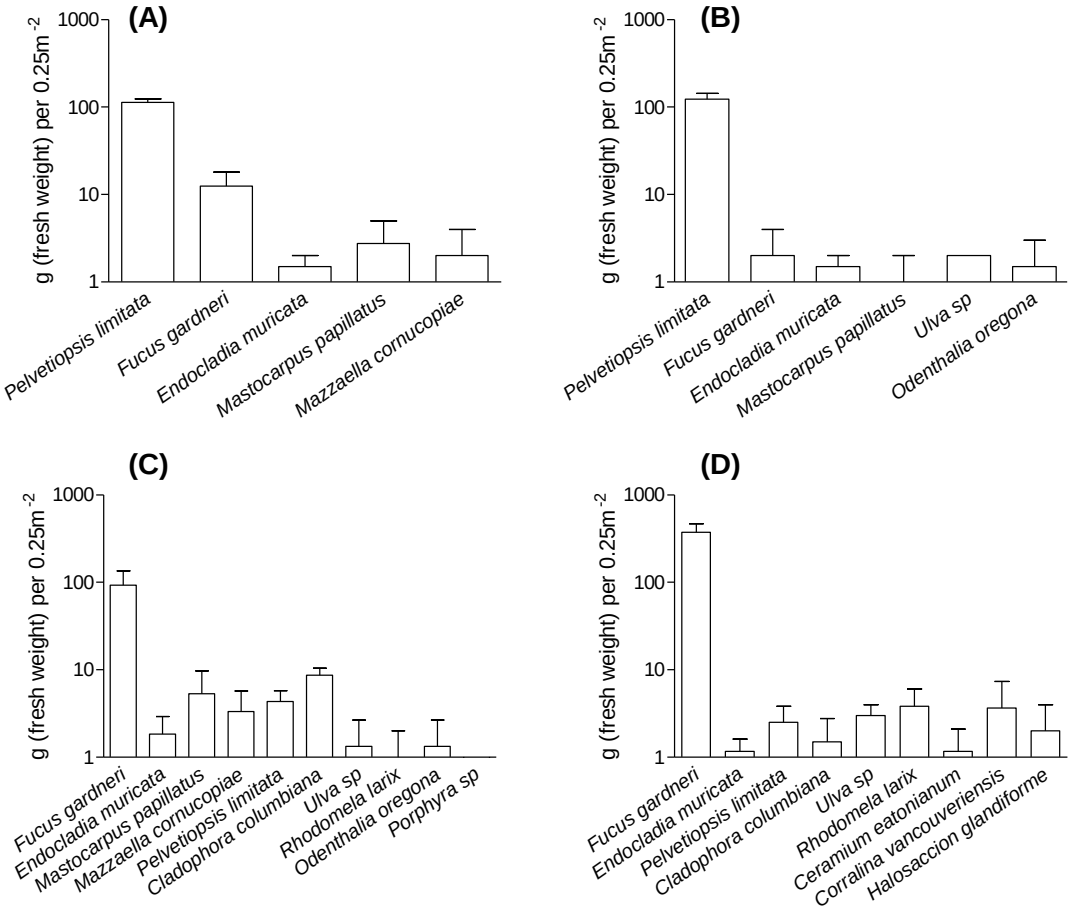

Figure 5.7. Average biomass (±SE; fresh weight per 0.25m^2) of mid shore and mid-high shore macroalgal assemblages in Oregon. Graphs show the diversity and biomass of the high-mid shore *Pelvetiopsis limitata* at Fogarty Creek (A) and Yachats reef (B), as well as, the mid shore *Fucus gardneri* at Fogarty Creek (C) and Yachats reef (D). Y-axis shown as log scale.

Since long term plots could not be harvested after each visit, an estimate of biomass without removing algae was necessary. To do this, a relationship between macroalgal percentage cover and biomass was generated by measuring biomass of a number of *H. banksii* dominated assemblages (Fig. 5.8). The relationship between total percent cover and biomass indicates a good fit (r^2 = 0.9). Although this relationship indicates a relatively good fit, it is likely that assemblages with less than 50% cover or above 220% may show a slightly different relationship. However, biomass was not extrapolated for any assemblages with a total species cover below 50% or above 230%.

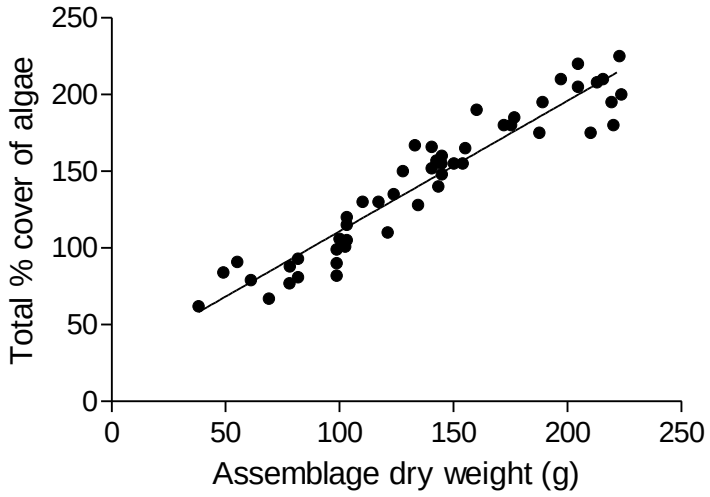

Figure 5.8. Relationship between assemblage dry weight and overall percent cover of algae in 25cm diameter plots. Regression equation (y= 0.85x + 25.78, r^2 = 0.90) used to calculate dry weight of non-harvested assemblages.

5.3.2. *Effects of canopy disturbance on production and community composition in mid shore assemblages*

Species composition and relative cover varied significantly between removal treatments and sampling period (Fig. 5.9). In the minus *C. torulosa* treatment, approximately 20-50g (fresh weight) *C. torulosa* was removed and approximately 300-500g (fresh weight) of *H. banksii* was removed from the minus *H. banksii* treatments. In the control treatment, overall algal diversity ranged between 10-12 species over the two years of sampling, and while the cover of the dominant species varied little, there was much more variation in the presence and total cover of many rare species. Algal diversity ranged between 7-9 species in the minus *C. torulosa* treatment. Interestingly, even 24 months after removal, no *C. torulosa* had recruited into the 'minus *C. torulosa*' plots. Algal diversity ranged between 5-9 species in the minus *H. banksii* treatment. Unlike the minus *C. torulosa* treatment, *H. banksii* started recruiting into the 'minus *H. banksii*' plots after 6 months and reached values close to control levels at 24 months.

Primary production over time in the three treatments shows large variation in primary production between treatments and over time (Fig. 5.10). Firstly, all intact assemblages over the study show the two-stage rise in production with irradiance (as discussed in Chapter 4) as do the minus *C. torulosa* treatments, despite being less pronounced in the early stages. Dynamics of production in the winter (3 months) show

slightly higher light use efficiency at lower irradiance levels, compared to data from the summer or spring months (0, 6, 12 and 24 months). At the beginning of the experiment, removal of the less dominant fucoid *C. torulosa* showed a marked drop in primary production at high irradiance, whereas the loss of *H. banksii* caused a drop in primary production throughout the irradiance range when standardised by reef area (g C m^{-2} h^{-1}). However, when standardised by dry weight (mg gDW^{-1} h^{-1}) production was similar in all treatments at most irradiances, except at high irradiance, where the intact assemblage was more productive. Primary production after the removal of *C. torulosa* recovered to control levels after approximately 6 months using both methods of standarisation. However, primary production after the removal of *H. banksii* recovered to control levels after 2 years only when standardised by mg C gDW^{-1} h^{-1}. The recovery of primary production to control levels in the minus *H. banksii* treatments corresponds to a recovery in the abundance of *H. banksii* into the treatment plots (as seen in Fig. 5.9). Whereas the recovery of primary production in the minus *C. torulosa* treatment is not associated with recruitment of *C. torulosa*. All curves fitted are third-order polynomial plots. When data are standardised by reef area, there is a more dramatic effect of canopy removal on production, but when standardised by dry weight much of the variation can be accounted for by the loss of biomass. However, at high levels of irradiance there is a noticeable difference between the canopy control and removal treatments.

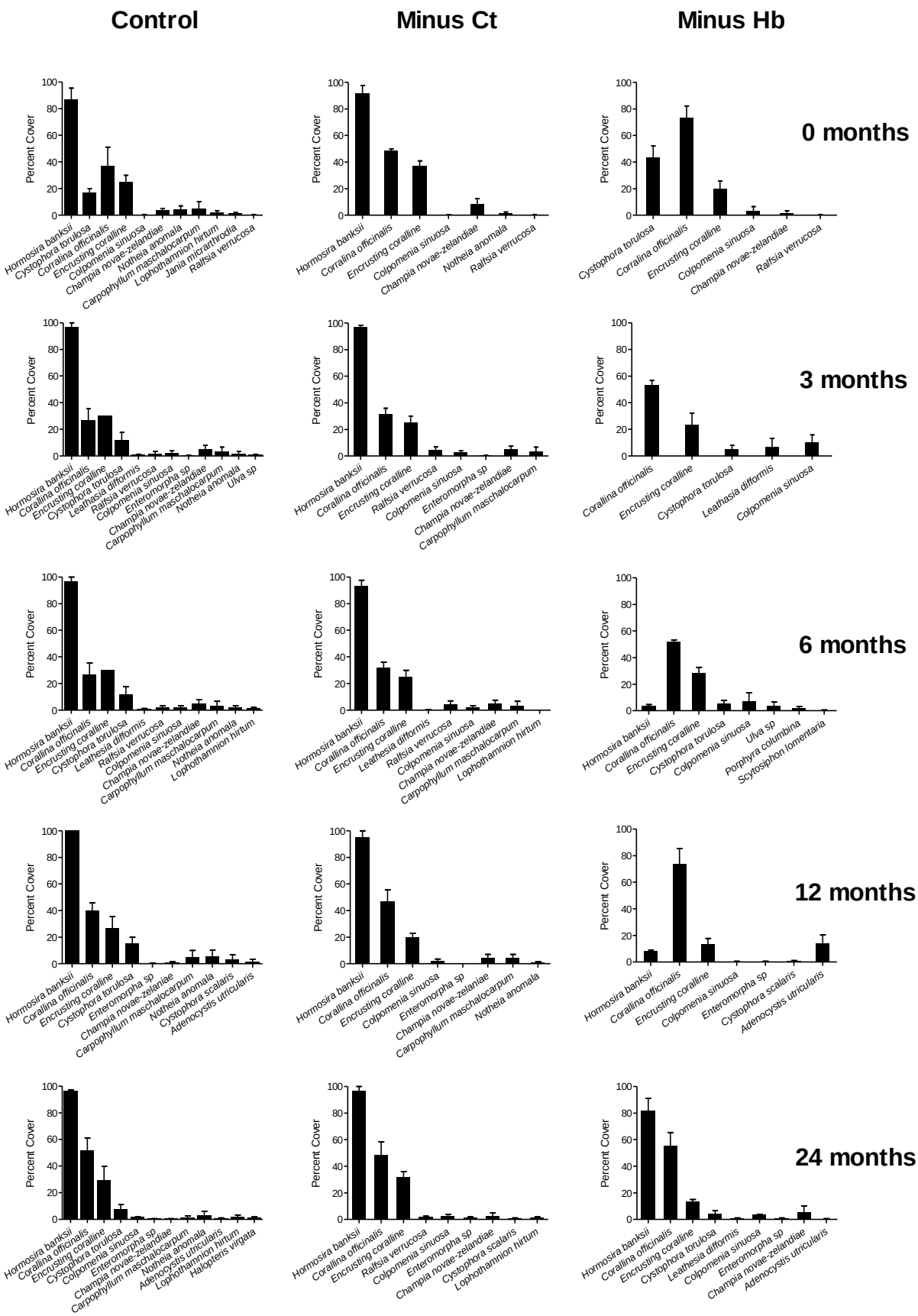

Figure 5.9. Macroalgal species composition and cover (±SE) in control plots, minus *C. torulosa* (minus Ct) plots and minus *H. banksii* (minus Hb) plots. Data taken at time zero (initially after removal), 3 months, 6 months, 12 months and 24 months after removal.

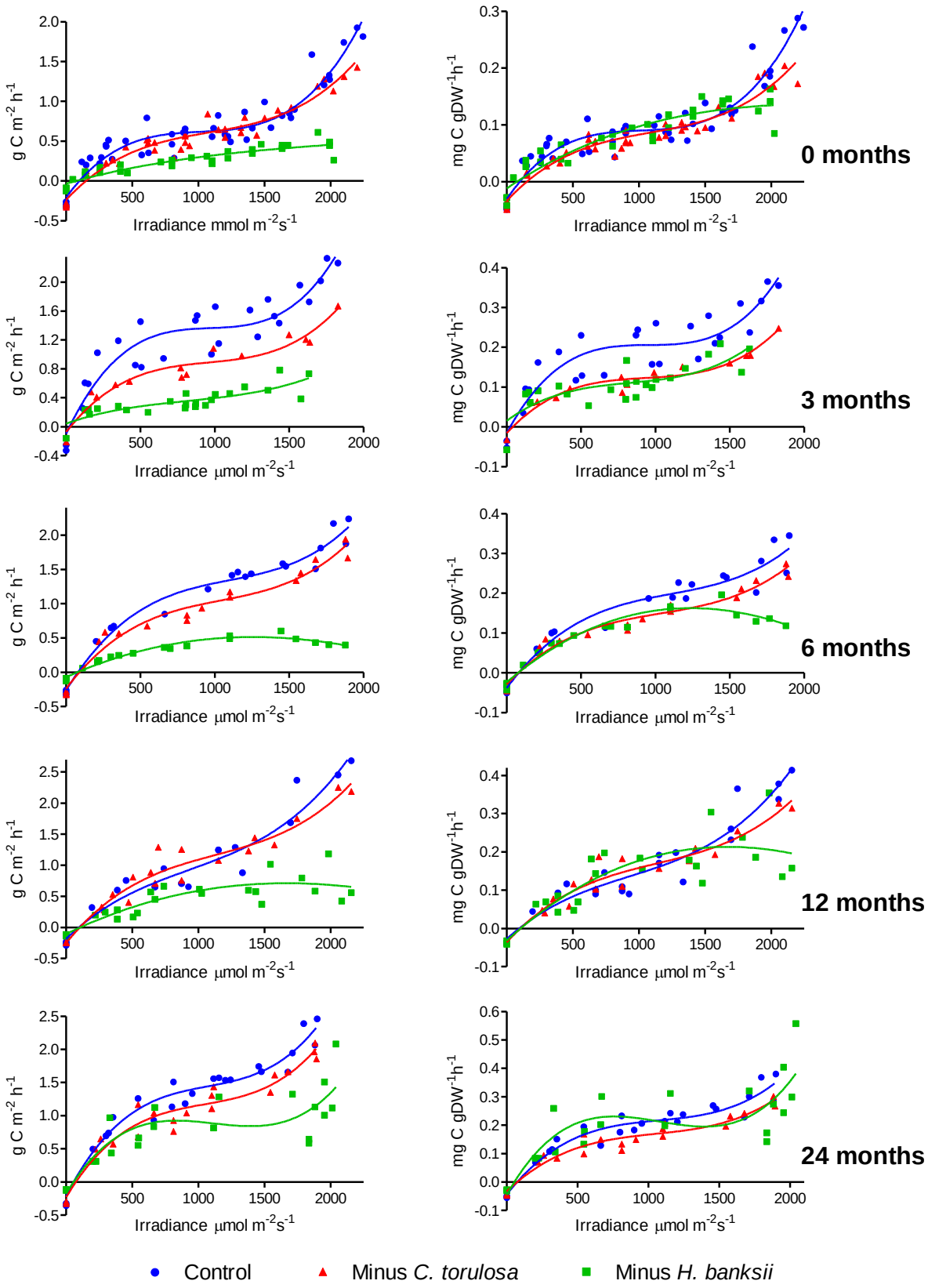

Figure 5.10. Primary production and irradiance of *in situ* macroalgal assemblages, including intact assemblages and the canopy removal treatments. Production shown for two units of standardisation, reef area (g C m^{-2} h^{-1}) and dry weight (mg C gDW^{-1} h^{-1}), at 0, 3, 6, 12, and 24 months after canopy removal.

Removal of the subcanopy species (primarily *C. officinalis* and its epiphytes) at time zero, meant the loss of a large amount of the total richness compared to control assemblages (Fig. 5.11). However, after 6 months, four macroalgal species *Colpomenia bulosa*, *Champia novae-zelandiae*, *Leathasia difformis* and *Lophothamnion hirtum*, had recruited into the 3 replicate plots. Although the cover of *H. banksii* and *C. torulosa* reduced over the 6 months, non-geniculate coralline algae increased, as did total algal cover due to the recruitment of new species.

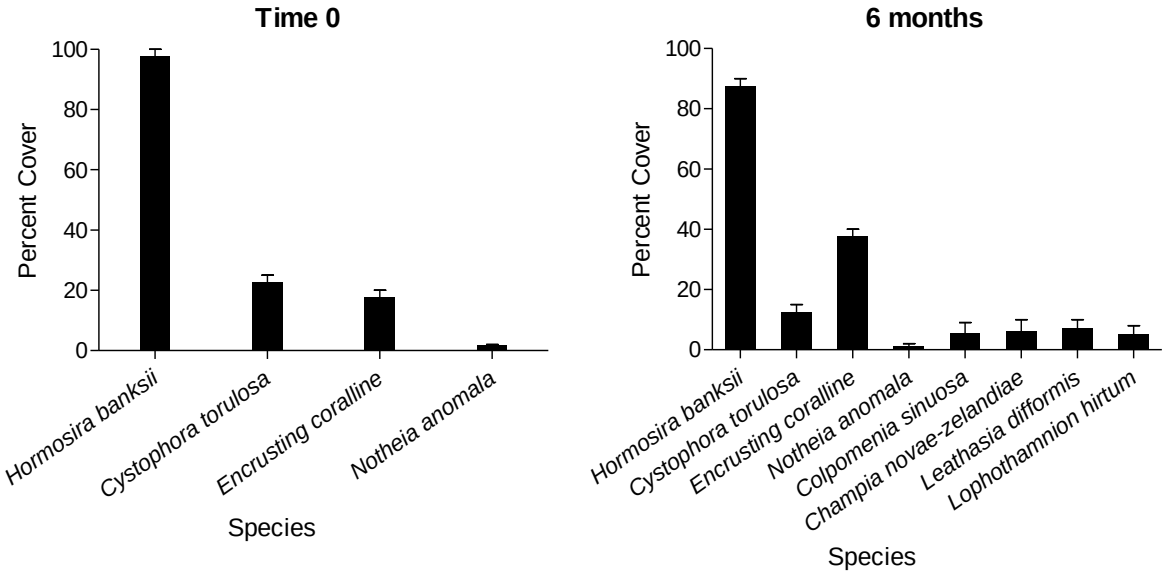

Figure 5.11. Effects of subcanopy removal on species composition and cover (±SE), directly after removal (time 0) and 6 months after removal.

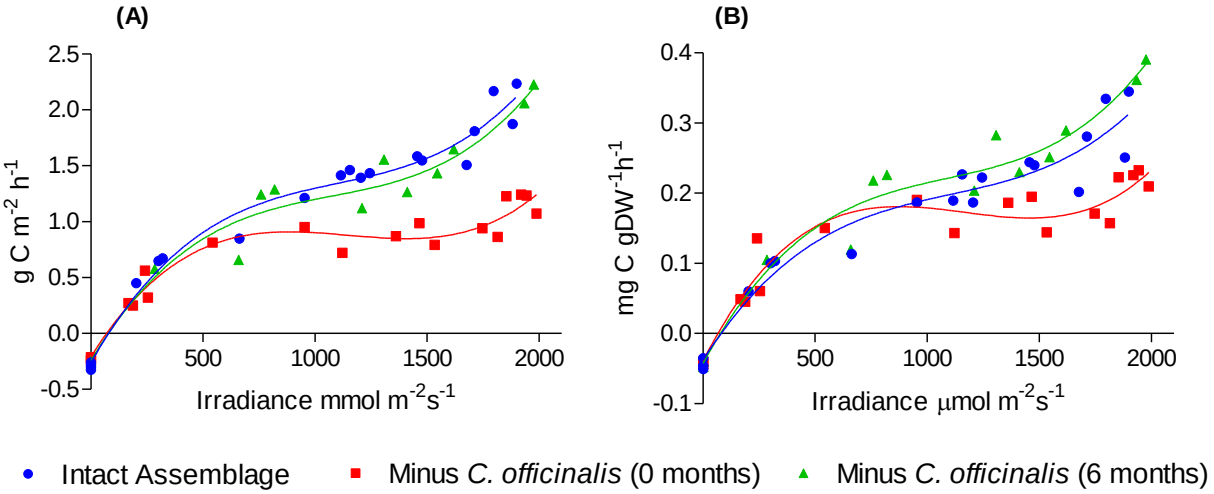

Figure 5.12. Effects of *C. officinalis* removal on primary production of *H. banksii* dominated macroalgal assemblages at 0 and 6 months after removal. Data are standardised by (A) g C m^{-2} h^{-1} (reef area) and (B) mg C gDW^{-1} h^{-1}(dry weight).

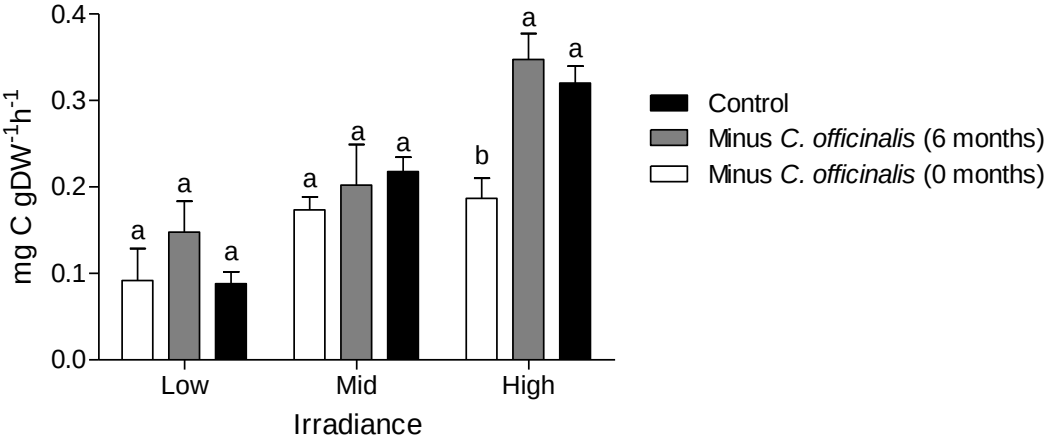

Figure 5.13. Effects of *C. officinalis* removal on production (±SE) compared to control assemblages at time zero and 6 months after removal. Production shown at high (1500-2000 µmol m^{-2} s^{-1}), mid (600-1200 µmol m^{-2} s^{-1}) and low irradiance (50-300 µmol m^{-2} s^{-1}). Tukey's post-hoc test shows difference between treatments, within irradiance levels. Significant difference between groups indicated by different letter.

Initial removal of subcanopy species from the *H. banksii*-dominated assemblages resulted in a marked change in primary production throughout most of the irradiance range (Fig. 5.12). At high irradiance there was a significant fall in overall primary production in the removal plots compared to control values initially (Fig. 5.12, 5.13). After 6 months, the loss in production from the removal of *C. officinalis* had been regained. Two-way ANOVA on the effects of three irradiance levels, high (1500-2000 µmol m^{-2} s^{-1}), mid (600-1200 µmol m^{-2} s^{-1}) and low (50-300 µmol m^{-2} s^{-1}) and the three treatments (control, minus *C. officinalis* 0 months, and minus *C. officinalis* 6 months) showed that both irradiance ($F_{2,18}$ = 36.9, $p < 0.0001$) and treatment ($F_{2,18}$ = 6.9, $p < 0.01$) had a significant effect on production. Bonferroni post-hoc tests show differences between minus *C. officinalis* 0 months, and minus *C. officinalis* 6 months, at high irradiance (t = 4.5, $p < 0.001$). There was also a significant difference between control and minus *C. officinalis* 0 months at high irradiance (t = 3.4, $p < 0.01$). There was no significant differences between treatments at mid and low irradiance.

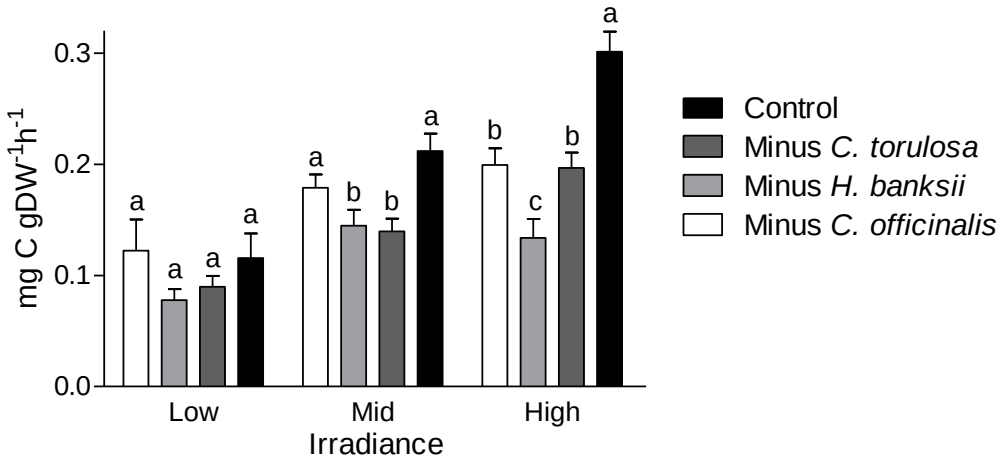

Figure 5.14. Effects of canopy and subcanopy removal on production (±SE) at (1500-2000 µmol m^{-2} s^{-1}) mid (600-1200 µmol m^{-2} s^{-1}) and low irradiance (50-300 µmol m^{-2} s^{-1}). Tukey's post-hoc test shows difference between treatments, within irradiance levels. Significant difference between groups indicated by different letter.

Species loss from *H. banksii*-dominated assemblages resulted in a fall in production, particularly at high irradiance (Fig. 5.14). At low irradiance the control treatment and the minus *C. officinalis* treatments were more productive than the minus *C. torulosa* and minus *H. banksii* treatments, but the difference was statistically insignificant. Two-way ANOVA showed a significant interaction effect between canopy treatment and irradiance ($F_{6,56}$ = 3.1, p < 0.01) on production. Bonferroni post-hoc tests showed that at mid irradiance, the control treatment was significantly more productive than the minus *C. torulosa* (t = 3.6, p < 0.01) and minus *H. banksii* (t = 3.3, p < 0.01) treatments. Furthermore, at high irradiance the control treatment was significantly higher than all treatments (minus *C. torulosa*, t = 4.2, p < 0.001; minus *H. banksii*, t = 6.4, p < 0.001; minus *C. officinalis*, t = 4.1, p < 0.001).

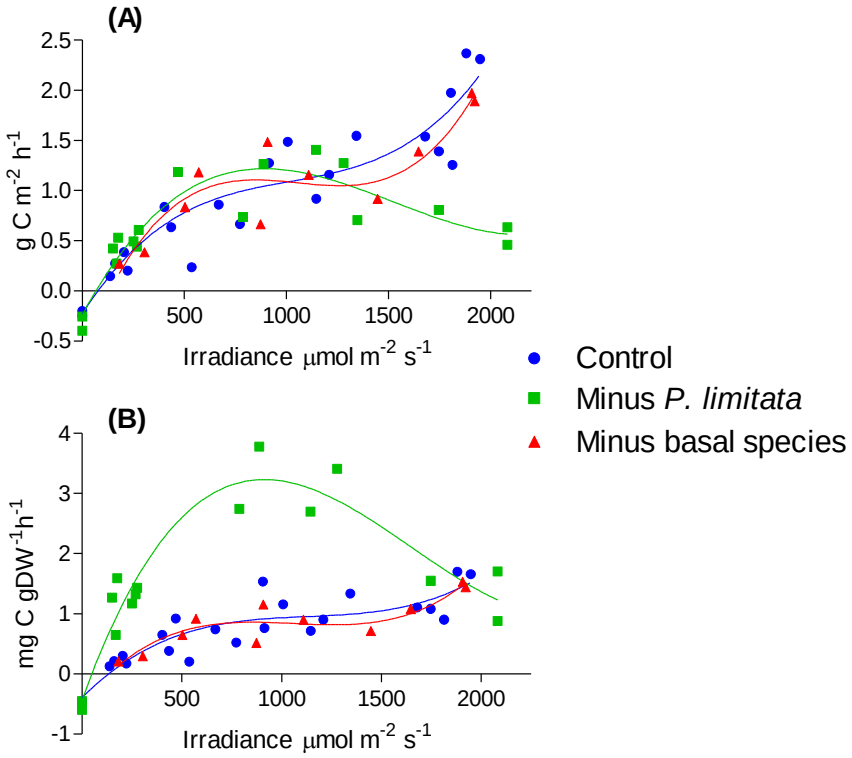

Figure 5.15. Effects of canopy and subcanopy removals from *P. limitata*-dominated assemblages on production across irradiance in Oregon. Graphs show production standarised by (A) g C m^{-2} h^{-1} (reef area) and (B) mg C gDW^{-1} h^{-1} (dry weight).

The loss of the basal species from *P. limitata* dominated assemblages resulted in a minor change in production (Fig. 5.15). Although the loss of *P. limitata* canopy caused a fall in production at high irradiance when standardised by reef area, when standardised by dry weight, production increased significantly throughout the irradiance range, except at high irradiance where control and minus *P. limitata* were similar. The impacts of canopy and subcanopy loss from assemblages dominated *F. gardneri* indicated a fall in production after the removal of all components when standardised by reef area, but the results varied when standardised by dry weight (Fig. 5.16). The loss of the basal species caused a fall in production at high irradiance levels when standardised by both reef area and dry weight. Removal of *P. limitata* resulted in a fall in production per reef area, but production remained unchanged when standardised by dry weight. Canopy removal resulted in a rise in production at mid irradiance, when standardised by dry weight, but at high irradiance the loss of *F. gardneri* canopy caused a fall in production, regardless of standardisation.

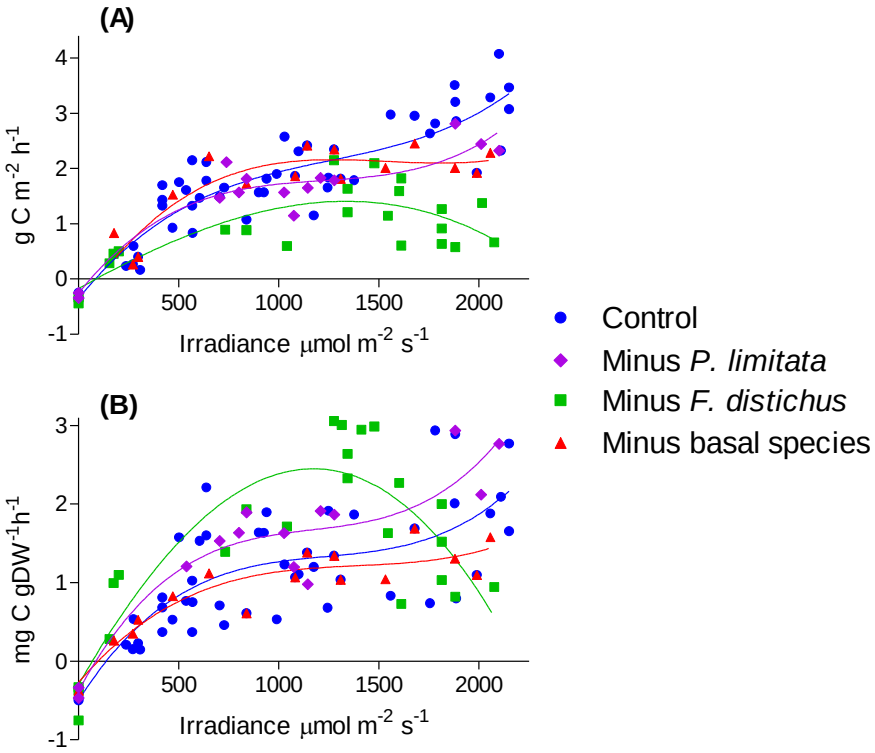

Figure 5.16. Effects of canopy and subcanopy removals from *F. distichus*-dominated assemblages on production across irradiance in Oregon. Graphs show production standarised by (A) g C m^{-2} h^{-1} (reef area) and (B) mg C gDW^{-1} h^{-1}(dry weight).

Two-way ANOVA and Bonferroni post-hoc tests showed no significance between treatments at high irradiance in *P. limitata* dominated assemblages, but did show significantly higher production at high irradiance in control *F. gardneri*-dominated assemblages compared to the minus basal species and minus *F. gardneri* treatments (Fig. 5.17). Also, canopy removal treatments in both assemblages caused an increase in production at low and mid irradiance levels. Two-way ANOVA showed a significant effect of treatment (*F. gardneri*, $F_{3,47} = 5.3$, $p < 0.001$; *P. limitata*, $F_{2,31} = 34.4$, $p < 0.0001$), irradiance (*F. gardneri*, $F_{2,47} = 52.3$, $p < 0.0001$; *P. limitata*, $F_{2,31} = 25.3$, $p < 0.0001$), and an interaction effect (*F. gardneri*, $F_{6,47} = 6.8$, $p < 0.0001$; *P. limitata*, $F_{4,31} = 13.2$, $p < 0.0001$).

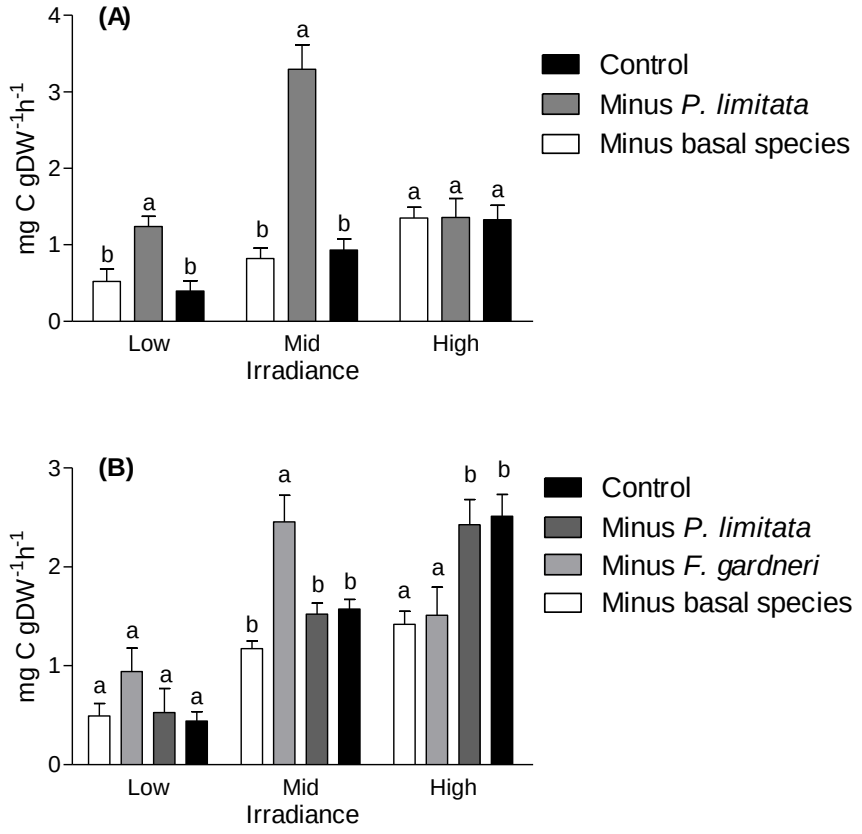

Figure 5.17. Effects of canopy and subcanopy removal on production (±SE) at (1500-2000 µmol m^{-2} s^{-1}) mid (600-1200 µmol m^{-2} s^{-1}) and low irradiance (50-300 µmol m^{-2} s^{-1}). Graphs show effects of removals in assemblages dominated by (A) *Fucus gardneri*, and (B) *Pelvetiopsis limitata*. Tukey's post-hoc test shows difference between treatments, within irradiance levels. Significant difference between groups indicated by different letter.

When the effects of canopy and subcanopy loss were compared between New Zealand and Oregon there were some major differences, particularly in the direction of change after the removal of some components (Table 5.4). Firstly, at mid and low irradiance, the loss of canopy species caused a rise in production per gram dry weight in Oregon assemblages (*F. gardneri* and *P. limitata*), but a fall in production in New Zealand assemblages (*H. banksii*). Furthermore, the loss of the subcanopy fucoid *C. torulosa* from New Zealand assemblages had a much larger effect than the loss of *P. limitata* from *F. distichus* dominated assemblages. However, the loss of basal species from *F. gardneri* and *H. banksii* dominated assemblages caused a significant fall in production at high irradiance.

Table 5.4. The effects of assemblage component removal on primary production (pp) compared to controls. Change is calculated as the fall in production relative to the production of the control at three levels of irradiance. Positive pp % change indicates a fall in production and a negative % change indicates a rise in production. Statistical significance is derived from Two-way ANOVA's done on Fig. 5.14 and 5.17.

Assemblage component removed		Dominant species					
		Hormosira banksii		*Fucus gardneri*		*Pelvetiopsis limitata*	
	Irradiance	% change in pp	Statistically Significant	% change in pp	Significant	% change in pp	Statistically Significant
Subcanopy	Low	25.7	no	-19.3	no	-	-
	Mid	34.0	yes	3.5	no	-	-
	High	33.2	yes	3.4	no	-	-
Canopy	Low	34.3	no	-113.4	no	-212.1	yes
	Mid	31.6	yes	-55.8	yes	-257.8	yes
	High	55.5	yes	39.8	yes	-2.3	no
Basal species	Low	-5.2	no	-120.2	no	-30.2	no
	Mid	15.6	no	25.4	no	11.8	no
	High	33.2	yes	43.8	yes	-1.9	no

The loss of *C. torulosa* from *H. banksii* dominated assemblages resulted in an initial fall in production at low, mid and high irradiance, but recovered close to control levels within approximately 12 months (Fig. 5.18). The effects of removing *H. banksii* on production are much more pronounced at high irradiance and was approximately half that of control values. At most levels of irradiance recovery after the loss of *H. banksii* only occured after 24 months. The effects of species removal were much larger at high irradiance, whereas at low irradiance there was very little difference between control and removal treatments. Although control production varied significantly at the mid-irradiance range, minus *C. torulosa* and minus *H. banksii* treatments were very similar.

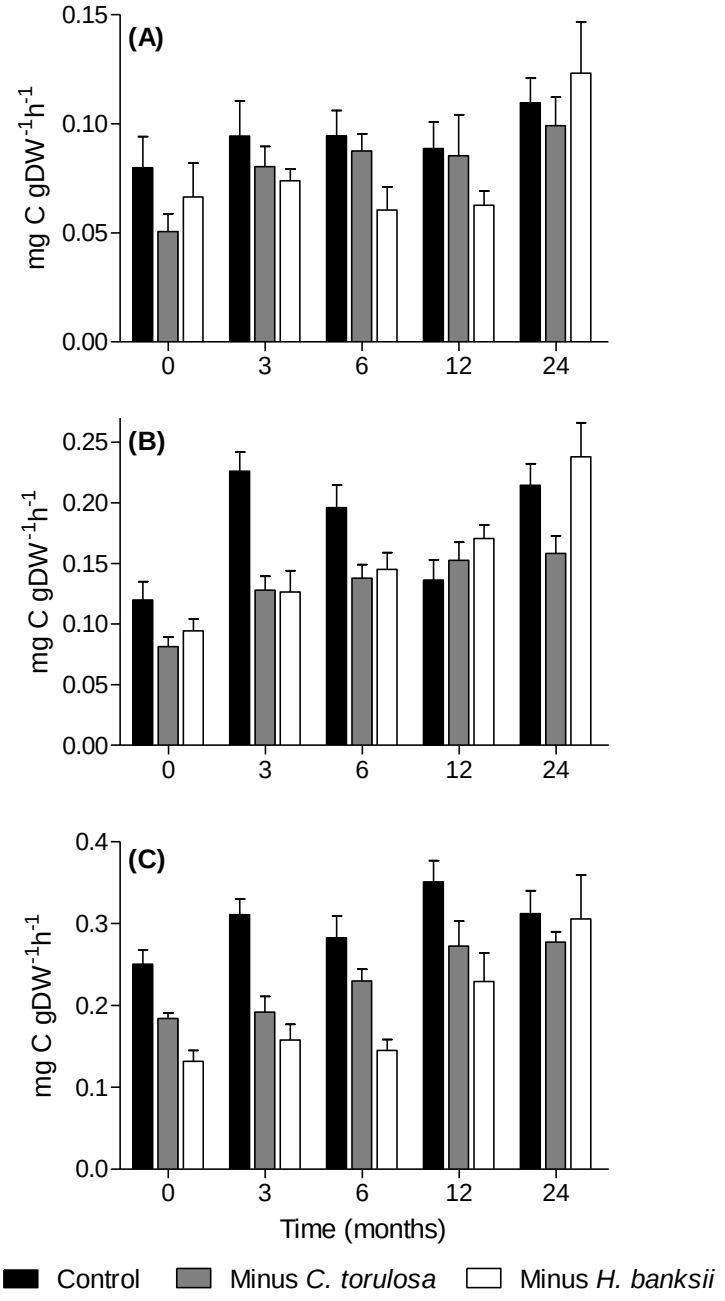

Figure 5.18. Maximum primary production (±SE) of *H. banksii* assemblages and the effects of canopy and subcanopy removal over time, after the initial disturbance at time zero. Graphs show production at (A) low irradiance 50-350 µmol m^{-2} s^{-1}, (B) mid irradiance 700-1100 µmol m^{-2} s^{-1}, and (C) high irradiance 1500+ µmol m^{-2} s^{-1}.

Data from Fig. 5.18 were used to analyse the effects of irradiance, treatment and time on production of *H. banksii* dominated macroalgal assemblages. Factorial ANOVA on the effects of irradiance (low irradiance 100-250 µmol m^{-2} s^{-1}, mid irradiance 600-1200 µmol m^{-2} s^{-1}, and high irradiance 1500+ µmol m^{-2} s^{-1}), treatment (control, minus *C. torulosa* and minus *H. banksii*), and time (0, 3, 6, 12 and 24 months) on production

indicate a significant effect of all factors (Table 5.5). All two-way interaction effects irradiance x treatment, irradiance x time, and treatment x time were also significant.

Table 5.5. Factorial ANOVA table showing the effects of irradiance, treatment and time on production of *H. banksii* dominated assemblages.

Factorial ANOVA	SS	Degr. Of Freedom	MS	*F*	p
Intercept	6.04	1	6.04	2860.6	<0.0001
Irradiance	1.04	2	0.52	246	<0.0001
Treatment	0.12	2	0.06	28.8	<0.0001
Time	0.25	4	0.06	29.3	<0.0001
Irradiance*Treatment	0.08	4	0.02	8.9	<0.0001
Irradiance*Time	0.04	8	0.01	2.4	0.015
Treatment*Time	0.06	8	0.01	3.8	<0.001
Irradiance*treatment*Time	0.04	16	0.002	0.97	0.48
Error	0.44	207	0.002		

5.3.3. *Pathway analysis on the effects of canopy removal on mid shore assemblages*

Canopy removal had a large effect on the change in community composition after 12 months compared to control plots (Fig. 5.19). After 12 months the composition of control assemblages had changed very little with an average distance moved of 11.09 units (calculated as a vector between time 0 and 12 months). In contrast, the removal plots changed dramatically over 12 month, with an average distance moved of 45.3 units.

The pathway analysis on the cascading effects of canopy removal on temperature, community composition and production indicated a significant flow-on effect. Pathway analysis indicated that the removal of canopy had an effect on both community composition and temperature (Fig. 5.20). However, only the effect of canopy removal on temperature was significant (Standardised regression weight = -0.88, $p < 0.0001$). Consequently, temperature had a significant effect on community composition (Standardised regression weight = -1.12, $p < 0.0001$), which then significantly affected production (Standardised regression weight = -0.84, $p < 0.0001$). The link between temperature and production was removed, because although temperature may affect production, the direct effects of temperature were not tested.

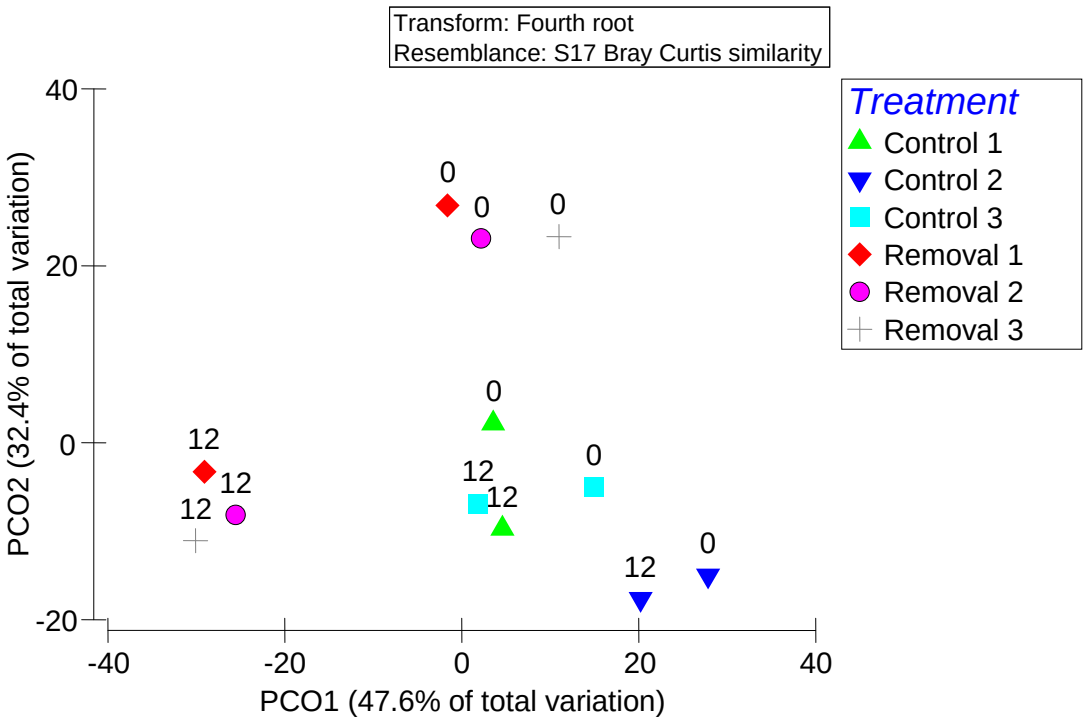

Figure 5.19. PCO plot showing the change in community composition after 12 months in canopy removal and control plots. The distance between the vectors for each replicate plot was used to determine the relative change caused by canopy removal in the pathway analysis (Fig. 5.21).

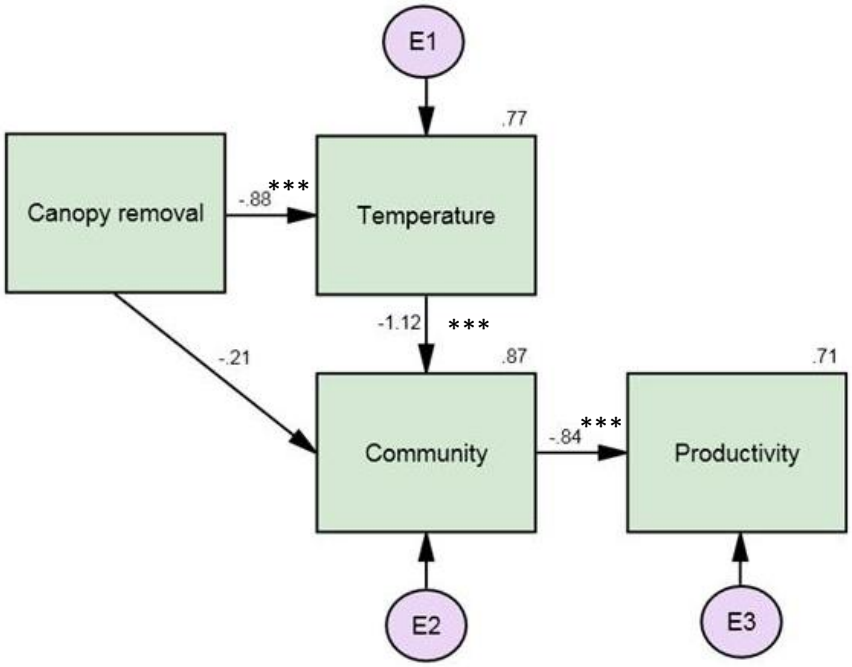

Figure 5.20. Pathway analysis showing the impacts of canopy removal on temperature and community structure, and the flow on effects on primary production. Significant effect of one factor on another shown by * (P < 0.0001). External, un-tested factors indicated by circles (E1, E2 and E3).**

5.3.4. *Primary production across a shore-height gradient and the effects of canopy loss across that gradient*

Primary production across a gradient of shore height with changing species dominance showed that low-shore species were more productive per reef area, throughout most of the irradiance range (Fig. 5.21 A). The high shore *H. banksii* assemblage had lower production than the *C. torulosa* assemblage and co-dominant *H. banksii* and *C. torulosa* assemblage (per dry weight). Although the co-dominant assemblage (*H. banksii* and *C. torulosa*) was less productive than the *C. torulosa* assemblage throughout most of the irradiance range, production at high irradiance was very similar between the two. However, the high shore *Porphyra spp* assemblage did show slightly higher production than most of the species at low to mid irradiance levels, but showed much lower production at high irradiance (per dry weight). *D. antarctica*, which borders the intertidal, subtidal fringe had the highest production of all the assemblages throughout the irradiance range. The relationship between production and biomass for species at different shore heights showed that the high shore species *Porphyra spp* has the highest production for its biomass (at irradiance intensities below 1500 µmol m^{-2} s^{-1}, Fig. 5.21 B), but is one of the least productive species per metre squared. Also, the species lowest on the shore, *D. antarctica*, had the lowest production for its biomass at low irradiance, but second highest at high irradiance. The three mid-shore species showed a slight relationship of increasing production per biomass down the shore-height gradient at both high and low irradiance (Fig 5.21 B). Two-way ANOVA shows a significant difference between species (reef area, $F_{4,155} = 17.9$, $p < 0.0001$; dry weight, $F_{4,155} = 151$, $p < 0.0001$) and a significant effect of irradiance (reef area, $F_{6,155} = 22.2$, $p < 0.0001$; dry weight, $F_{6,155} = 68.1$, $p < 0.0001$). There was also a significant interaction between species and irradiance (species x irradiance, dry weight, $F_{24,155} = 5.1$, $p < 0.0001$; dry weight, $F_{24,155} = 13.2$, $p < 0.0001$). The increasing levels of production down the shore, were most likely due to differences in biomass between assemblages, but may also be related to species composition of the assemblages.

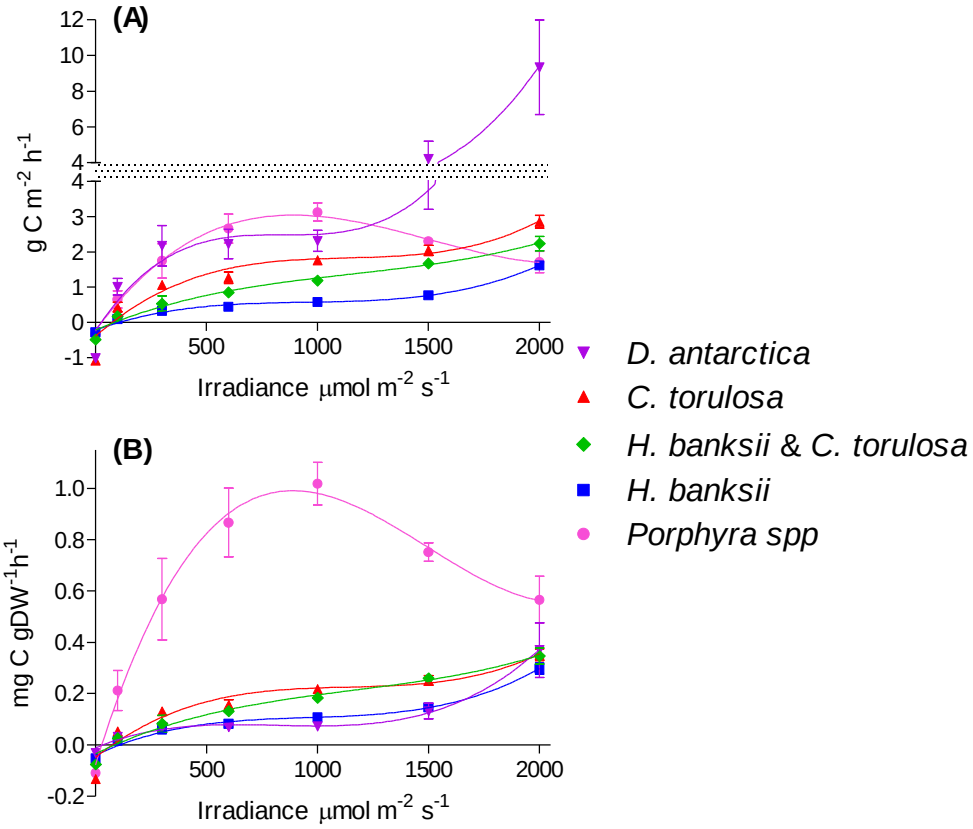

Figure 5.21. Primary production (±SE) against irradiance in five assemblage types which occur down a shore height gradient. The high shore *Porphyra spp*, mid/high shore *H. banksii*, equal dominance of *H. banksii* and *C. torulosa* in the mid shore, the low shore *C. torulosa* dominant assemblage and the very low shore *D. antarctica*. Data are standardised by reef area (A) g C m^{-2} h^{-1} and dry weight (B) mg C gDW^{-1} h^{-1}.

Analysis of the differences in primary production between shore heights indicated higher production in the low shore assemblages at high and low irradiance when standardised by reef area (Fig 5.22). However, when standardized by dry weight of algae, the trend of increasing production in the low shore disappeared, and the high shore *Porphyra spp* had the highest relative production and *D. antarctica* the second highest. When standardised by reef area, at high irradiance the low shore assemblages were significantly more productive than the high shore *H. banksii* dominated assemblage. Two-way ANOVA showed a significant effect of irradiance ($F_{1,49}$ = 88.9, p < 0.0001), and a significant effect of shore-height ($F_{4,49}$ = 26.8, p < 0.0001) on primary production. There was also a significant effect of irradiance across the shore-height gradient (height x irradiance, $F_{4,49}$ = 6.3, p < 0.0001). Bonferroni post-hoc tests also showed that at high irradiance there were significant differences between *D. antarctica* and *H. banksii* (*t* =

6.5, p < 0.001), *D. antarctica* and co-dominant of *H. banksii* and *C. torulosa* (*t* = 5.2, p < 0.001), *D. antarctica* and *C. torulosa* (*t* = 5.5, p < 0.001), as well as *D. antarctica* and *P. columbina* (*t* = 5.9, p < 0.001).

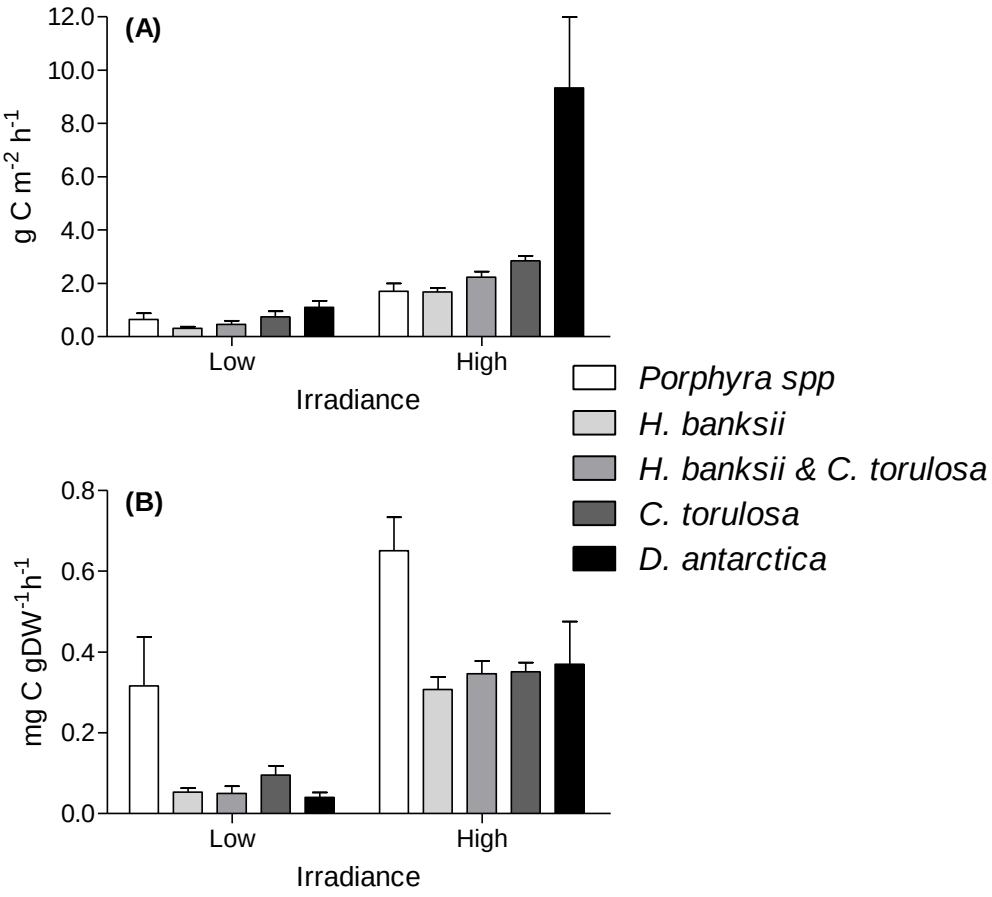

Figure 5.22. Primary production (±SE) at high and low irradiance of 5 assemblages from various shore heights. Shore heights are in order from highest (*Porphyra spp* to lowest (*D. antarctica*). Data are standardised by reef area (A) g C m^{-2} h^{-1} and dry weight (B) mg C gDW^{-1} h^{-1}.

The same trend of higher primary production in low shore assemblages was seen in Oregon macroalgal communities (Fig. 5.23). The high shore assemblage dominated by *P. limitata* had the lowest primary production at low and high irradiance, the mid shore *F. gardneri* slightly more productive and the low shore *Hedophyllum setchell* showing the highest production. Although there was no significant difference between the treatments, there was a significant effect of irradiance (Two-way ANOVA, $F_{1,24}$ = 35.6, p < 0.0001).

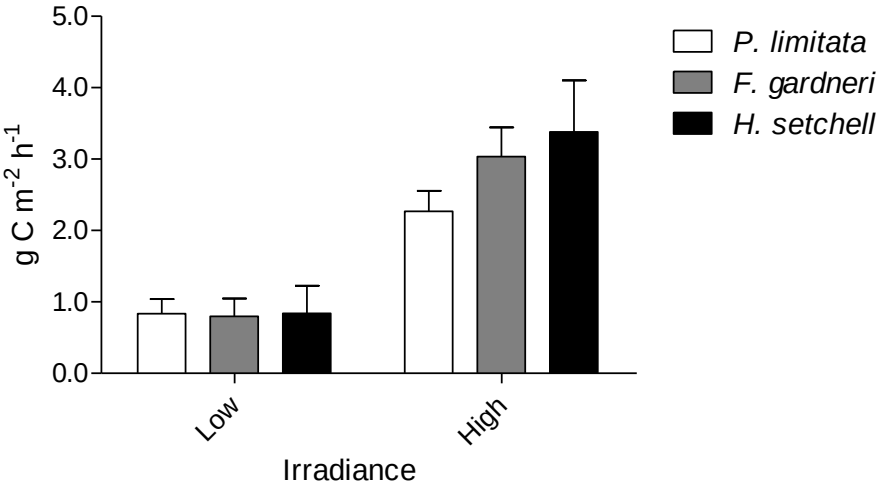

Figure 5.23. Primary production (±SE) at high and low irradiance of 3 canopy forming species from Oregon, USA. Species occur at distinct tidal heights with *P. limitata* dominating the high-shore, *F. gardneri* the mid-shore and *H. setchell* the low-shore.

In the mid-low shore where *H. banksii* and *C. torulosa* occurred in equal dominance, diversity was relatively high, with several species occurring in relatively high abundance (Fig. 5.24 A). However, slightly lower on the shore where *C. torulosa* was dominant, the assemblages were more diverse and had almost 100% canopy cover of *C. torulosa* (Fig. 5.24 B). Several other species including, *C. officinalis*, *H. banksii*, *C. novae-zealandiae*, *H. virgata* and *L. hirtum* also had relatively high cover.

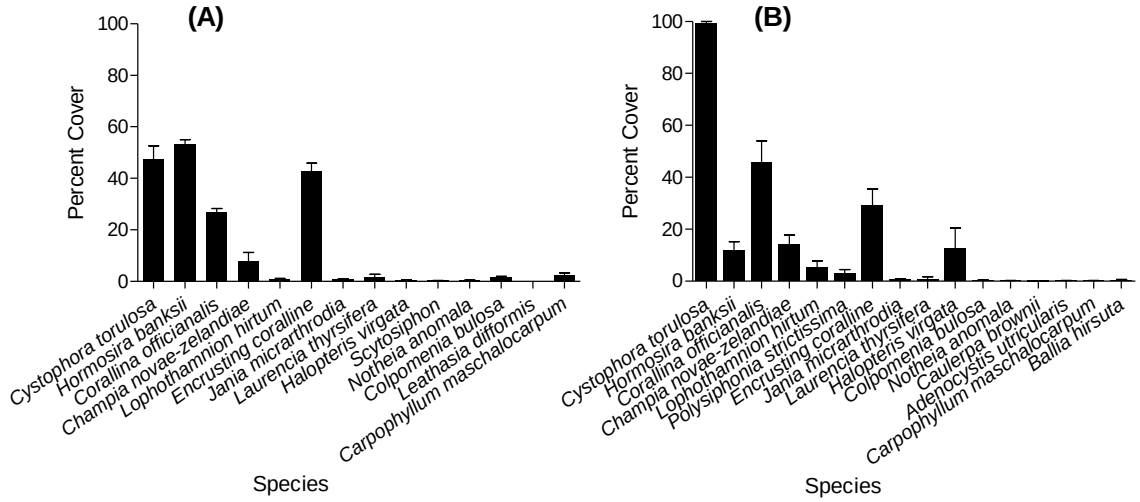

Figure 5.24. Species composition and cover (±SE) of mid shore plots co-dominated by *H. banksii* and *C. torulosa* (A) and low shore plots dominated by *C. torulosa* (B).

The effects of canopy and subcanopy removal down a shore-height gradient had mixed results depending upon the dominant species (Fig. 5.25). One-way ANOVA indicated a significant effect of treatment in the mid shore, $F_{2,12} = 26.7$, $p < 0.0001$, low-mid shore, $F_{2,12} = 3.7$, $p < 0.05$, but not in the low shore. The direct effects of species loss in the mid shore showed that removal of the dominant *H. banksii* and the less dominant *C. torulosa* significantly reduced primary production compared to control values (Tukey's post-hoc test, minus *H. banksii*, $q = 10.3$, $p < 0.001$; *C. torulosa*, $q = 4.7$, $p < 0.05$). In the low-mid shore, the loss of *H. banksii* had a slight effect on primary production, but this drop was statistically insignificant, even though this species occurs in equal amounts to *C. torulosa*, which caused a significant fall in primary production when removed ($q = 3.8$, $p < 0.05$). In the low shore, not even the loss of the dominant canopy species *C. torulosa* caused a significant fall in primary production, although production was slightly lower on average without *C. torulosa*.

Interestingly, the loss of the dominant *C. torulosa* from the low shore assemblage had less of an effect on assemblage production than its loss from the low-mid shore assemblages where it was co-dominant with *H. banksii*. In fact, the loss of *C. torulosa* had close to the same effect on assemblage primary production regardless of its dominance prior to its removal. Two-way ANOVA comparing the effects of *H. banksii* and *C. torulosa* canopy loss across the shore-height gradient showed a significant effect of removal treatment ($F_{2,40} = 8.1$, $p < 0.001$) and shore height ($F_{2,40} = 5.7$, $p < 0.001$). Bonferroni post-hoc tests showed that the loss of *C. torulosa* was not significantly different between shore heights (Table 5.6). However, the loss of *H. banksii* was significantly different between shore-heights. The removal of *H. banksii* had a more significant effect on overall primary production higher up the shore, whereas the loss of *C. torulosa* had the same effect regardless of where it is found and its dominance.

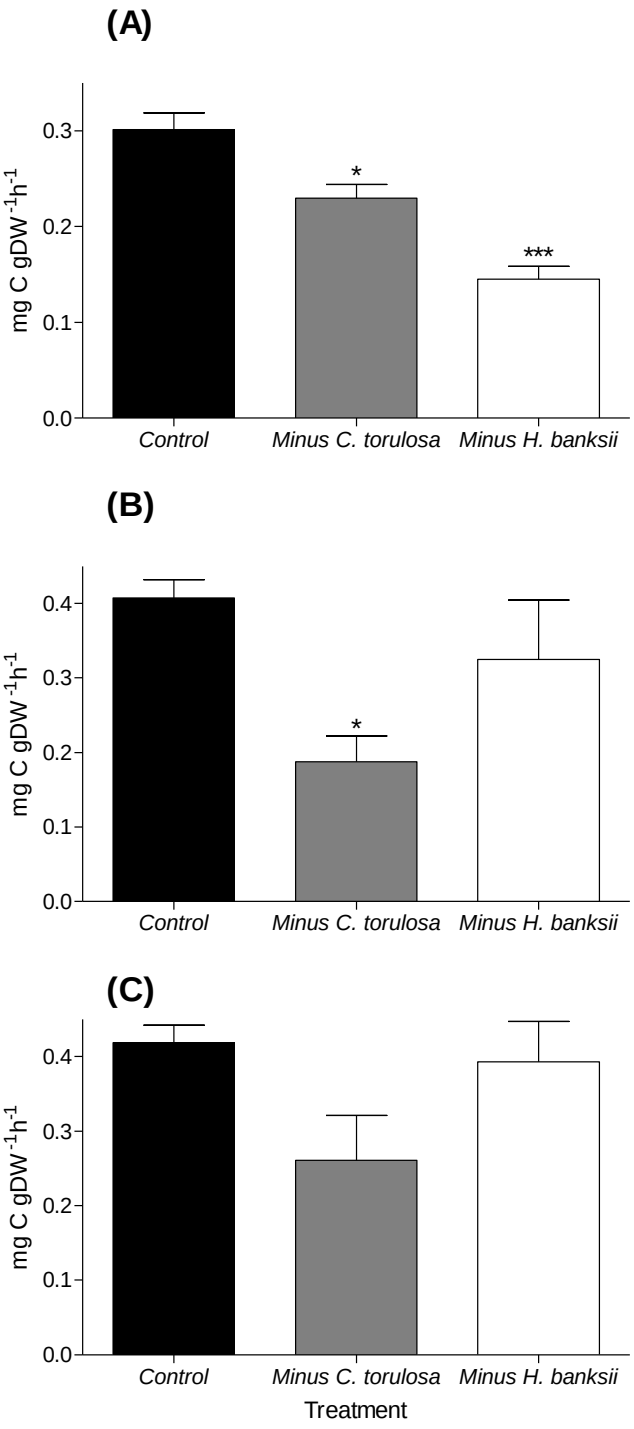

Figure 5.25. Effects of *H. banksii* and *C. torulosa* removal on primary production (±SE) at high irradiance 1500-2000 µmol m^{-2} s^{-1} down a shore height gradient. Communities dominated by, mid-high shore *H. banksii* (A), mid shore co-dominance of *H. banksii* and *C. torulosa* (B), and low shore *C. torulosa*. (significant difference from control indicated by *, p < 0.05 *, p < 0.001 *).**

Table 5.6. Two-way ANOVA and Bonferroni post-hoc test analysis on the effects of canopy removal in assemblages dominated by *H. banksii* (Hb), *C. torulosa* (Ct) and equal amounts of each on primary production across a shore-height gradient of changing species composition. Significant p-value shown by < 0.05, non-significant shown by 'ns' (when non-significant, *t*-values are not applicable, n/a).

Significant difference between treatment, and dominant species		Co-dominance			*C. torulosa*		
		Control	Minus *C. torulosa*	Minus *H. banksii*	Control	Minus *C. torulosa*	Minus *H. banksii*
H. banksii	p	ns	ns	< 0.05	ns	ns	< 0.01
	t	n/a	n/a	2.9	n/a	n/a	3.5
Equal Hb & Ct	p	-	-	-	ns	ns	ns
	t	-	-	-	n/a	n/a	n/a

5.4. Discussion

5.4.1. *In situ primary production of macroalgae and the effects of canopy and subcanopy disturbance*

Primary production of macroalgal assemblages showed a marked change in light use dynamics from summer to winter. Although maximum production of the assemblage remained relatively constant, production at lower irradiance was higher in winter than in summer. This was most likely due to increased photosynthetic pigment content in the winter to compensate for low irradiance levels. Evidence for this was seen in arctic macroalgae living beneath sea-ice (Aguilera et al. 2002), and in symbiotic dinoflagellates within reef building corals (Warner et al. 1996). In both cases, chlorophyll content was higher during winter or low irradiance conditions. This may be a mechanism to enhance primary production efficiency during lower light periods, or the lower pigment during summer months may be a protective mechanism. Regardless of the mechanism, the higher pigment content within the canopy algae during winter months was also associated with a significant rise in primary production at lower irradiance.

The initial effects of species removal are that canopy and subcanopy loss significantly reduced overall primary production when standardised by reef area. This was the case for New Zealand and Oregon assemblages, despite major differences in subcanopy composition. However, when production is standardised by dry weight of algal material, the removal of the canopy from *Fucus gardneri* and *Pelvetiopsis limitata* dominated assemblages showed a very different relationship. With the loss of the

dominant canopy species, production was significantly enhanced at low and mid irradiance. This suggests that there was a high amount of competition between canopy and subcanopy species for light, and at low and mid irradiance, the canopy may almost completely shade the subcanopy algae. This relationship was not seen in New Zealand assemblages, and was most likely due to differences in subcanopy composition and canopy structure. The thick, flat thalli of *F. gardneri* may have a larger effect on shading of the subcanopy assemblage than the narrow and tall *Hormosira banksii* thalli. Furthermore, Oregon assemblages had a diverse understory assemblage dominated by fleshy red algae (such as *Mazzaella cornucopiae* and *Mastocarpus papillatus*), whereas the understory of *H. banksii* was dominated by calcareous turfing algae (*Corallina officinalis*). Calcareous coralline algae are some of the least productive algae per weight, whereas fleshy red algae are some of the most productive (Littler & Littler 1980; Littler & Arnold 1982). Therefore, it is not surprising that this diverse understory significantly increased production in Oregon assemblages. However, at high irradiance there was a significant photoinhibition of these subcanopy assemblages and in the *F. gardneri*-dominated assemblages, production per biomass was higher with the canopy intact at high irradiance. Also, in ecological terms, the production per area was significantly higher in intact assemblages. Therefore, despite the rich and productive subcanopy of these assemblages, the loss of the canopy has significant consequences for overall community and ecosystem production.

The removal of subcanopy and basal species also had similar effects in New Zealand and Oregon assemblages, with the loss of *P. limitata* from *F. gardneri* dominated assemblages, and *Cystophora torulosa* loss from *H. banksii* dominated assemblages causing a fall in production. Although the loss of *P. limitata* from *F. gardneri* assemblages caused only a minor drop in production, the loss of basal species caused a significant fall in production in both New Zealand and Oregon assemblages. After the removal of *C. officinalis* from New Zealand assemblages, the recruitment of several ephemeral species caused a significant rise in production, suggesting that these species are vital to maintaining production of these intertidal assemblages, particularly at high irradiance.

In *H. banksii*-dominated assemblages, the loss of canopy species caused a major decline in production that lasted almost 2 years. Recovery of production after the loss of the canopy occurred only when the canopy species had recruited back into the assemblage at relatively high density. Canopy recovery of *H. banksii* in larger removals has been

shown to take longer than two years in certain cases (Underwood 1998; Underwood 1999; Lilley & Schiel 2006) and has major implications for the resilience of intertidal macroalgal assemblages. The cascading effects of canopy loss on temperature, community composition and production indicate a vital role of the canopy in ameliorating stress to the subcanopy assemblage. The loss of subcanopy fucoids, although resulting in a significant fall in production, only lasted for 6-12 months. Furthermore, the recovery of production after the loss of subcanopy fucoids and subcanopy turfs was not associated with their recruitment, but the recruitment of other macroalgal species. Recovery of community production without regaining the species removed from the assemblages shows a degree of redundancy within these assemblages. Although, *C. officinalis* or *C. torulosa* may not be functionally replaced *per se*, their contribution in terms of primary production is certainly replaced by other species. Conversely, primary production after the loss of *H. banksii* did not recover until *H. banksii* had recruited back into the assemblages suggesting it has no functional equivalent within the mid shore zone. Canopy forming fucoids have been considered as autogenic engineers or foundation species due to their role in maintaining diversity (Bertness et al. 1999; Schiel 2006), but this study suggests that their role in primary production is also key to overall ecosystem function.

The removal of the canopy causes a cascading effect through an increase in temperature, a change in community composition and a significant and prolonged drop in primary production. The recovery of primary production is only reversed when the canopy has recruited back into the assemblage. The long recovery time of fucoid algae has significant consequences for the recovery of intertidal assemblages (Underwood 1998; Schiel & Taylor 1999; Lilley & Schiel 2006). Increasing human disturbance has the potential to severely affect the cover and function of canopy forming macroalgae. Furthermore, one of the predicted consequences of climate change over the next 100 years is an increase in storm intensity and possibly frequency (Walsh & Ryan 2000; Knutson & Tuleya 2004; Webster et al. 2005; Trenberth 2005). This may have severe consequences on intertidal canopy forming algae which are immediately and intensely impacted by physical disturbance. Large scale losses of macroalgal canopies could have major consequences on the primary production of marine systems, and have the potential to be long term shifts in community composition and biomass output.

5.4.2. *Primary production across a shore-height gradient*

Macroalgal assemblages show a general trend of higher primary production in the low shore assemblages, although when standardised by dry weight, the order of highest relative production changes to the highest shore species *Porphyra spp*. However, this is most likely attributable to the very low biomass of *Porphyra spp*, and the very high biomass of species such as *Durvillaea antarctica*. Although *Porphyra spp* are very productive per gram dry weight, it is important to note that they only occurs in high densities for 3 months of the year, whereas the other species are perennial. Calculating primary production over an annual basis may therefore shift the balance in favour of the high biomass fucoid assemblages. Furthermore, primary production per area is more relevant to ecosystem energy budgets and is used often in the ecological literature (Miller et al. 2009). When considered as per area of reef surface, the low-shore assemblages are undoubtedly more productive because of the higher biomass within these assemblages, which has been shown to be the main predictor of primary production in *Macrocystis pyrifera* forests (Reed et al 2008). The lower irradiance environment of the low shore is associated with a higher efficiency of light use, but at high irradiance there are greater levels of photoinhibition in the low shore species (Chapter 2). However, photoinhibition is not exhibited in any fucoid assemblages as it is in single thalli and overall production is compensated for by the entire assemblage. The photoinhibition exhibited by *Porphyra spp* is most likely associated with the lack of community structure and low diversity. Therefore, at high irradiance similar light levels are reaching all algal material, as opposed to being attenuated through a structured assemblage. This results in photoinhibition due to excessive irradiance in the *Porphyra spp* assemblage, but the fucoid assemblages mitigate this through diversity and complementarity effects.

The intertidal zone has a very strong gradient of physical stress, often over very short distances and, therefore, it provides an ideal model to test the effects of physical stress on the spatial and temporal variability of ecosystems (Connell 1972). Gradients of physical stress have been shown to have large effects primary production. For example, an increasing salinity gradient negatively affects growth rates and production of mangrove trees (Sherman 2003). Also, phytoplankton primary production can increase along gradients of increasing nutrient input near river sources (Lohrenz et al. 1990). In terms of algal production across a shore-height gradient, two studies found greater photosynthetic capacity in high shore algae compared to low shore algae (Gómez et al. 1997; Skene

2004). This is opposite to the general relationship found in my study, but is most likely due to differences in standardisation, as these studies estimate production on a per weight basis. Despite the potential confusion associated with the standardisation of data, the ecologically significant value for primary production is per area, not per weight. The higher production of the low shore is a significant phenomenon in these assemblages and indicates a potential enhancement of production with decreasing physical stress. Energetic investment in photo-protective and desiccation resistant mechanisms must represent a significant drain on growth rates of high-shore algae. Furthermore, release from these stresses in the low shore and longer immersion allows assemblages to reach higher biomass, resulting in higher production per reef area.

5.4.3. *Functional replacement and redundancies in intertidal macroalgal assemblages*

There is considerable controversy about the contribution of individual species to overall ecosystem functioning (Lawton 1994). However, the importance of overall diversity is gaining momentum in the ecological literature (Duffy 2009), but with very little consideration of the relative importance of individual species. It has already been proposed that in the marine intertidal environment, ecosystem function is dependent upon canopy forming algae (Schiel 2006), and marsh macrophytes (Bertness & Leonard 1997). The loss of these species has a major effect on function and in some cases, these species have been shown to be functionally irreplaceable (Schiel 2006). The level of redundancy and the presence of 'key' species within communities is critical to our understanding of the potential impacts of species loss.

In this system, *H. banksii* is extremely important to overall ecosystem function, and its loss has major impacts on species diversity, community composition (Lilley & Schiel 2006; Schiel & Lilley 2007), and primary production. Furthermore, evidence suggests that despite the presence of functionally similar species (i.e., *C. torulosa*), no species can replace its role as a canopy dominant in the mid shore. Lack of functional replacement is not unique to this system and, in fact, such 'key' species have been proposed in several ecosystems. These species include autotrophic ecosystem engineers (Lawton 1994), bioturbators (i.e., earthworms; Carpenter & Kitchell 1993), nitrogen fixers (legumes; Spehn et al. 2002) and herbivores/predators (i.e., Parrotfish on coral reefs; Bellwood et al 2003). However, despite the lack of functional replacement of *H. banksii*, there was a large amount of redundancy in the subcanopy assemblage. Functional redundancies have also been reported in terrestrial systems, where the loss of a given

species can be compensated for by other species with similar functional traits (Symstad et al. 1998; Symstad & Tilman 2001). Although many subcanopy species may be redundant in terms of their contribution to primary production, redundancy is multi-faceted, operating at individual or population-levels and potentially involving several niche dimensions (Loreau 2004). Therefore, despite the presence of redundancies in primary production within the subcanopy assemblage, species may be providing other services to the ecosystem that are not measured in this study. However, the low abundance (spatially and temporally) and low biomass of these ephemeral species suggests that they have very similar roles within the intertidal environment and despite a large variation in the number and cover, there was very little change in community primary production over time. Therefore, it would seem plausible that although these low cover, low biomass ephemeral species are important for overall primary production, the identity and number of these species may have no appreciable effect on overall primary production.

The effects of canopy loss across a gradient of shore height shows a change in the consequences of species removal from mid shore to low shore. In the mid shore, loss of both canopy and subcanopy fucoids results in a significant fall in primary production, but in the low-mid shore only the loss of one species significantly affected production. Furthermore, the loss of *C. torulosa* had a greater effect on production when it was removed from low-mid shore plots where it is co-dominant with *H. banksii*, than removal from low shore plots where it was the dominant species. The loss of the dominant *C. torulosa* from the low shore had a statistically insignificant effect on production. This indicates that down a gradient of decreasing physical stress, assemblages are more resistant to canopy disturbance and potentially, overall species loss. This could be due to increasing species diversity down the shore, or may be associated with a general change in species composition.

The ability of the low shore assemblages to compensate for the loss of such a large amount of biomass suggests that there is some competition for light occurring between the canopy and subcanopy. Although, the subcanopy species are presumably low light adapted, once the canopy is removed, they are able to respond quickly to elevated irradiance. A similar problem has been observed in the terrestrial environment, where under harsher conditions (i.e., dryer conditions) there is a greater level of facilitation between canopy and subcanopy, but when environmental conditions are more benign, there is a greater level of competition between canopy and subcanopy (Holmgren et al. 1997). The ability of many species to persist in the mid shore is because of the macroalgal

canopy which ameliorates physical stress, but as a consequence they must inhabit a low light environment. Therefore, in any situation there must be both facilitation and competition occurring, but in the mid shore, the benefits of the canopy outweigh the cost of living in a shaded environment. However, in the low shore, the canopy may initially help in the establishment of propagules, but eventually the canopy may largely inhibit subcanopy growth. The loss of the canopy changes the irradiance environment, and leads to a large compensation in assemblage production by the subcanopy species. This may be analogous to the response of seedlings to newly created tree-fall gaps in forest ecosystems (Brokaw 1985; Canham 1988). In forest ecosystems, the production by the understory is significantly elevated by tree-fall gaps compared to the understory beneath normal canopy cover (Brokaw 1985; Canham 1988). The release of light competition may significantly enhance the production of subcanopy species in the low shore environment, but in the mid shore environment, the release from light competition is also associated with a lack of protection from desiccation stresses. Therefore, the low shore, subcanopy assemblages are in an ideal position to make use of the elevated irradiance levels, whereas the stresses of increased desiccation outweigh the benefits of elevated light in the mid shore. The relationship between facilitation and competition across a shore height gradient is illustrated in Fig. 5.26. This model has similarities to the adaptation of the Menge-Sutherland model (Menge & Sutherland 1976), adapted to include facilitation, by Bruno et al. (2003). The differences in this model lie mainly in the specificity for canopy-subcanopy interactions, which are defined by the effects of competition on production and the role of habitat forming species in ameliorating physical stress.

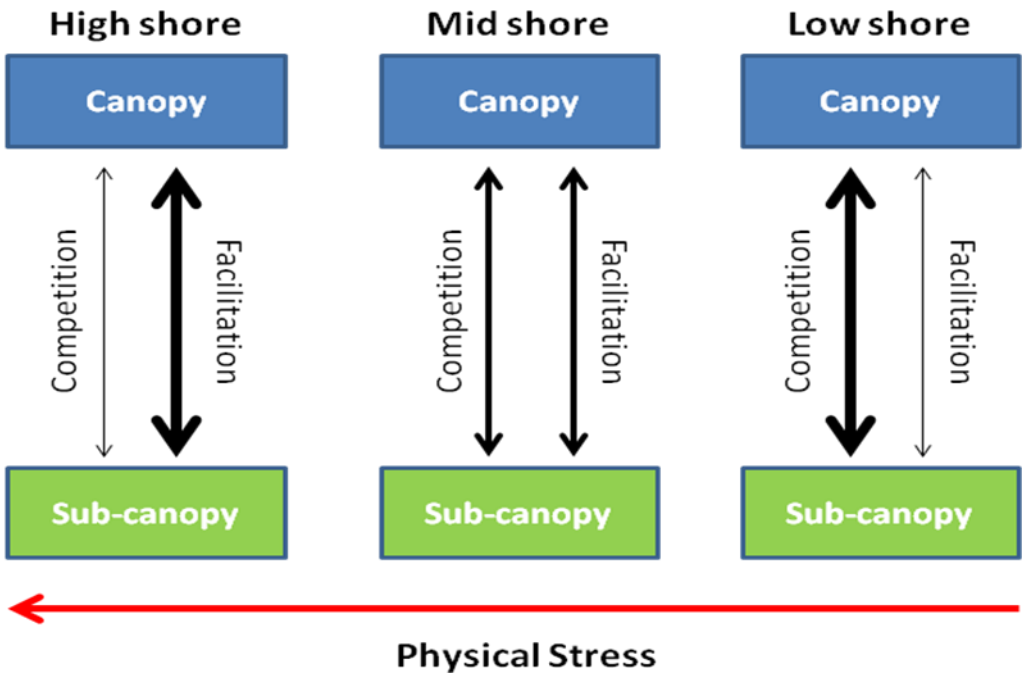

Figure 5.26. Model showing the effects of a physical stress gradient on the relative importance of competition and facilitation between canopy and subcanopy autotrophs. Strength of interaction depicted by thickness of arrow, thicker arrow represents stronger influence of that interaction. Modified from Menge-Sutherland model (Menge & Sutherland 1976) and Bruno et al (2003).

A growing amount of evidence suggests that although there may be a degree of functional redundancy within ecosystems, diversity still enhances function, or at least provides some form of buffering to species loss (Naeem & Li 1997; Duffy et al. 2001). It seems likely that ecological resilience is generated by the apparently redundant species that operate at different scales, thereby reinforcing function (Peterson et al. 1998). Evidence from this research suggests that in certain functional groups there may be some redundancy, but overall higher diversity in the low shore assemblages enhances primary production and buffers the effects of canopy loss. However, in the mid shore no redundancy was observed in terms of canopy species, and only the recovery of the one species, *H. banksii*, was associated with recovery of primary production back to control levels. These assemblages are, therefore, very vulnerable to disturbance and are likely to take several years to recover to typical assemblage composition and primary production. In high stress systems where facilitation is vitally important, the loss of 'key' species such as canopy forming autotrophs, is likely to have devastating consequences to ecosystem function, whereas benign environments may have few 'key species' and less facilitation.

5.4.4. *Summary*

This research indicates that canopy species are vital not only to amelioration of physical stress to the subcanopy, but also contribute to a significant proportion of overall assemblage primary production. At high irradiance intact assemblages were twice as productive as those where the canopy was removed, and 25% more productive than those where basal or subcanopy species were removed. Furthermore, following the loss of canopy species in the mid shore, assemblage production did not recover until the species removed (*Hormosira banksii*) recruited back into the assemblage. In contrast, recovery after the removal of the subcanopy species *Cystophora torulosa* and *Corallina officinalis* was not associated with their recruitment. This indicates a degree of redundancy in the subcanopy assemblage, but a key role of the canopy forming species.

Canopy and subcanopy removal across a gradient of shore height indicated an increasing level of compensation at lower shore levels. In low shore assemblages the loss of the dominant canopy species had very little effect on overall production compared to mid shore assemblages. Higher species richness in the low shore may increase the resilience of low shore assemblages to canopy disturbance.

This research indicates that mid shore assemblages are more vulnerable to disturbance and are less able to compensate for the loss of production, whereas low shore assemblages with higher species diversity are able to buffer the loss of dominant species. Identifying which systems are more susceptible to sustained losses may help environmental agencies identify the ecosystems or communities which are most vulnerable to anthropogenic disturbance.

Chronosequence of disturbance

Long-term effects of canopy disturbance on the community-state of macroalgal assemblages and the consequences to primary production

6.1. Introduction

All natural communities are exposed to many types of disturbance, the effects of which largely depend on their temporal and spatial scales and magnitude (Sousa 1984; Connell & Keough 1985). Disturbances such as wave action, grazing and human-mediated impacts, therefore, play a major role in structuring marine communities (Chapman & Johnson 1990). The timing and duration of disturbance events on macroalgal communities vary significantly on local and regional scales (Dayton 1985; Schiel & Foster 1986) and macroalgal assemblages often represent a mosaic of successional stages of recovery. Understanding how natural disturbances affect the composition and subsequent recovery of biological communities, therefore, underpins an understanding of how human disturbance might exacerbate community effects, the time trajectory of recovery, and whether there are shifts to alternative states (Suding et al. 2004). The recovery of communities to some form of pre-disturbed 'climax community' may be a relatively long process and in some cases it is not possible to monitor sufficient recovery over a typical research period (Dollar & Tribble 1993). To study long term recovery of biological communities effectively, studies must either be long-term, or use a mixture of patches that have been disturbed at varying times. This gives a mosaic of succession with replicates at different points in their recovery trajectory, effectively allowing a long term study over a short period, often referred to as a chronosequence (Dollar & Tribble 1993).

Chronosequences have been extensively used by ecologists to examine successional patterns where the long life span of species precludes time series observations of the entire successional sequence. A chronosequence can be referred to as a mosaic of patches that have been developing for various lengths of time following a known disturbance. Such observations have been useful in formulating models of succession in terrestrial plant communities (Wardle et al. 2004) and seagrass beds (Peterson et al. 2002). Despite the usefulness of chronosequences in understanding successional patterns in these communities, the relatively fast turnover of shallow coast macroalgal assemblages means that the effects of disturbance over time is often well understood (Chapman & Underwood 1998; Underwood 1998; Lilley & Schiel 2006). Furthermore, in certain cases after a major disturbance the community may not reach what is considered its 'climax state,' even after an extended period of time (Underwood 1998; Lilley & Schiel 2006). The switch to an alternative stable state has been suggested to occur in several rocky reef systems (Simenstad et al. 1978; Barkai & Branch 1988;

Johnson & Mann 1988; Petraitis & Dudgeon 1999; Petraitis & Latham 1999). Although, this is still a contentious issue, it seems that in some examples patches of rocky shore communities can remain in a different stable state following a major disturbance event (Underwood 1998; Petraitis & Dudgeon 1999; Petraitis & Latham 1999). Long-term successional processes following major disturbances may give valuable insight into the ability of macroalgal assemblages to recover, and their ability to reach what is considered a 'climax state.' Furthermore, the effects of successional trajectory on primary production in marine macroalgal assemblages has not been considered, and may help us understand the factors controlling ecosystem function and the functional roles of various species groups. Understanding how shifts in 'ecosystem state' affect ecosystem function will provide greater insights into the potential impacts of multiple stressors (i.e., canopy loss, desiccation stress, and sedimentation) on marine systems.

In many cases the first species lost to disturbance on shallow temperate reefs are the large canopy-forming species that experience considerable drag forces and can be removed completely or partially from the reef (Denny 1995; Blanchette 1996; Blanchette 1997; Underwood 1998; Schiel 2006). The effects of canopy loss on primary production over ecologically significant timescales will give important insight into the successional processes in macroalgal assemblages and the time required for disturbed assemblages to reach pre-disturbed levels of primary production. The aim of this experiment was to test the ability of macroalgal assemblages to recover to control (or predisturbed) levels and approach a 'climax state' or an alternative state. I test the null hypothesis that primary production of mid and low shore assemblages is unaffected by canopy removal and time since removal.

6.2. Methods

6.2.1. *Chronosequence experiment, standardisation and species cover*

Long-term removal experiments that examined the effects of canopy removal on assemblage composition were used as a basis for this study to test the consequences of canopy disturbance on primary production. This included the removal of canopy-forming macroalgal species at two tidal heights, mid shore and low shore. The mid shore *Hormosira banksii* removal experiment was set up in June 2002 at North reef Moeraki (Lilley 2004) to examine the role of *H. banksii* in ameliorating stress to the mid shore assemblages of subcanopy algae and invertebrates. The low shore *Durvillaea antarctica*

removal experiment was set up in March 2006 to examine the role of *D. antarctica* in shaping community composition. The mid shore removal experiment was monitored for 2 years and the low shore removal experiment was monitored for 4 years (Lilley 2004). Permanent markers on each replicate plot enabled the relocation of all treatments. In this study I tested the effects of canopy removal on primary production in these old experimental plots. Furthermore, new canopy removal treatments were set up in March (*H. banksii*) and September (*D. antarctica*) 2009 to examine the initial effects of canopy loss on production. This chronosequence of canopy disturbance to mid shore and low shore assemblages enabled a test of the time necessary for recovery from a major disturbance and the primary production of these old disturbed plots.

Incubations measuring primary production were done using the custom designed photo-respirometry chambers described in Chapter 3. These were sealed around target assemblages immediately prior to incubations and removed after incubations to limit any long term disturbance of the target assemblage. This allowed assemblages to be exposed to natural conditions and sampled over time. A chamber was set within each of three old canopy-removal areas, controls and new removal plots. A two compound epoxy resin was used to fill in deeper cracks within the substratum, but care was taken not to change the reef composition so much that pooling of water occurred. Before incubations were carried out, all visible invertebrates were removed from the assemblages within the chamber area. On flat surfaces, the only manipulation of the reef was drilling the holes for the rawl plugs.

For analysis of primary production, data were standardised by either grams dry weight of algal material (mg C gDW^{-1} h^{-1}) or by area of reef substratum (g C m^{-2} h^{-1}). Due to the long term nature of many of these experiments and the need for repeated sampling, the biomass of algal assemblages could not be directly measured. Therefore, an estimate of biomass was used to standardise production by grams dry weight. This was done by calculating the relationship between total percent cover of algae and dry weight using harvested algae from outside of treatment plots. Algae were harvested from an area of reef the same size as the chamber (i.e., a diameter of 25cm). Before removal from the substratum, the percent cover of all species was recorded. Algae were dried in a conventional oven for 24 hours at 50˚C and the dry weight recorded. A regression between percent cover and dry weight allowed the biomass of algae in permanent plots to be estimated by non-destructive measurements of percent cover. For convenience in presentation, areal estimates of primary production were standardised to a square metre.

As well as assessing primary production, the cover and diversity of species were measured at each sampling time in the mid and low shore. This was done so that primary production could be related to recovery and succession through time as the species composition changed. During primary production sampling, all macroalgal species within the experimental plots were recorded and their percentage cover estimated using a grided quadrat. Macroalgal species were only recorded if they were attached and covered an area equal to or greater than 0.5% of the quadrat. Multi-dimensional scaling plots (MDS) using PRIMER were used to visualize the variation in community structure between treatments over time. MDS plots were analysed using PERMANOVA (using 999 simulation permutations) analysis, as well as CLUSTER analysis using Simprof tests. For analysis all replicate plots (n = 3) were plotted independently, but for presentation replicate plots were averaged for each time period. Cover of *H. banksii* and *D. antarctica* were removed from MDS analysis, as is standard procedure in removal type experiments.

6.2.2. *Chronosequence of recovery in mid shore communities*

The chronosequence of recovery in mid shore communities was tested using the old experimental canopy removals (June 2002) and new removal plots, set up in October 2008. For the new removal treatments, *H. banksii* canopy was removed from 3, 0.25 m^{-2} areas, within which plots for the chambers were prepared. The old experimental removal treatments were larger at 3x3 m and within each of the three canopy-removal treatments a chamber plot was set up. When I began the primary production studies, the old canopy removal plots were 6.5 years old. The treatments for the experiment were, control, new removal (time zero after canopy removal), and old removal (6.5 years after canopy removal). These plots were sampled in spring 2008, autumn 2009 and spring 2009 giving the corresponding chronosequence of, time zero, 6 months, 12 months, 6.5 years 7 years and 7.5 years after canopy disturbance (Table 6.1). Furthermore, the effects of canopy loss on production over time were compared between Moeraki and Kaikoura. Data from Kaikoura was taken from Chapter 5, where *H. banksii* dominated assemblages were disturbed (*H. banksii* removed) and allowed to recover. Production was tested in *H. banksii* removal plots and control plots over two years.

To visualise the change in cover of the dominant species *H. banksii* and *Corallina officinalis* over time, I used data from the original removal experiment. These data were taken from the 3x3 m removal and control plots set up by Lilley (2004).

6.2.3. *Chronosequence of recovery in low shore communities*

As with *H. banksii* in the mid shore assemblages, old removal experiments of *Durvillaea antarctica* canopy enabled the investigation of the long-term impacts of canopy loss on assemblage primary production in the low shore. Three replicate plots, 2x2 m in size were cleared of all adult *D. antarctica* thalli in September 2006. Furthermore, three replicate new removal plots 0.5x0.5 m were cleared in September 2009. Incubations testing primary production in all treatments were carried out during spring 2009 and autumn 2010. This gave a chronosequence of time 0, 6 months, 2.5 and 3 years since canopy removal (Table 6.1). The removal of *D. antacrtica* was originally done at two sites North reef, Moeraki and Oaro reef, Kaikoura. However, primary production measurements were only done at North reef, Moeraki, because the very uneven limestone and conglomerate reef at Oaro rendered it impossible to attach the incubation chambers effectively. Due to the large size of *D. antarctica*, controls were set up around moderate sized plants (no taller than 50-60 cm), because larger ones would not fit inside chambers (see Fig. 6.1).

Table 6.1. Experimental treatments in the mid (*H. banksii*) and low shore (*D. antarctica*) including the date of canopy removal, when the primary production measurements were made and how that related to the chronosequence.

Shore Height	Treatment	Time of canopy removal	Time of PP sampling	Chronosequence (months)	No of replicates
Mid-shore	Control	-	Mar-09, Sep-09, Mar-10	-	3
	New removal	Oct-08	Mar-09, Sep-09, Mar-10	0, 6, 12	3
	Old removal	Jun-02	Mar-09, Sep-09, Mar-10	78, 84, 90	3
Low-shore	Control	-	Sep-09, Mar-10	-	3
	New removal	Sep-09	Sep-09, Mar-10	0, 6	3
	Old removal	Sep-07	Sep-09, Mar-10	30, 36	3

To visualise the change in cover of the dominant species *D. antarctica* and coralline algae over time, I used data from the original removal experiment. These data were taken from the 2x2 m removal and control plots set up by Schiel in 2006 (Unpublished data).

At Moeraki, abundance of the invasive alga *Undaria pinnatifida* increased markedly during the course of the *D. antarctica* removal experiment and was found in the removal and control treatments. To further test the potential role of this species in assemblage production, another incubation series was done on *U. pinnatifida* dominated

assemblages during spring 2009. Incubations were done on 3 replicate assemblages dominated by *U. pinnatifida* in the very low shore of North reef, Moeraki.

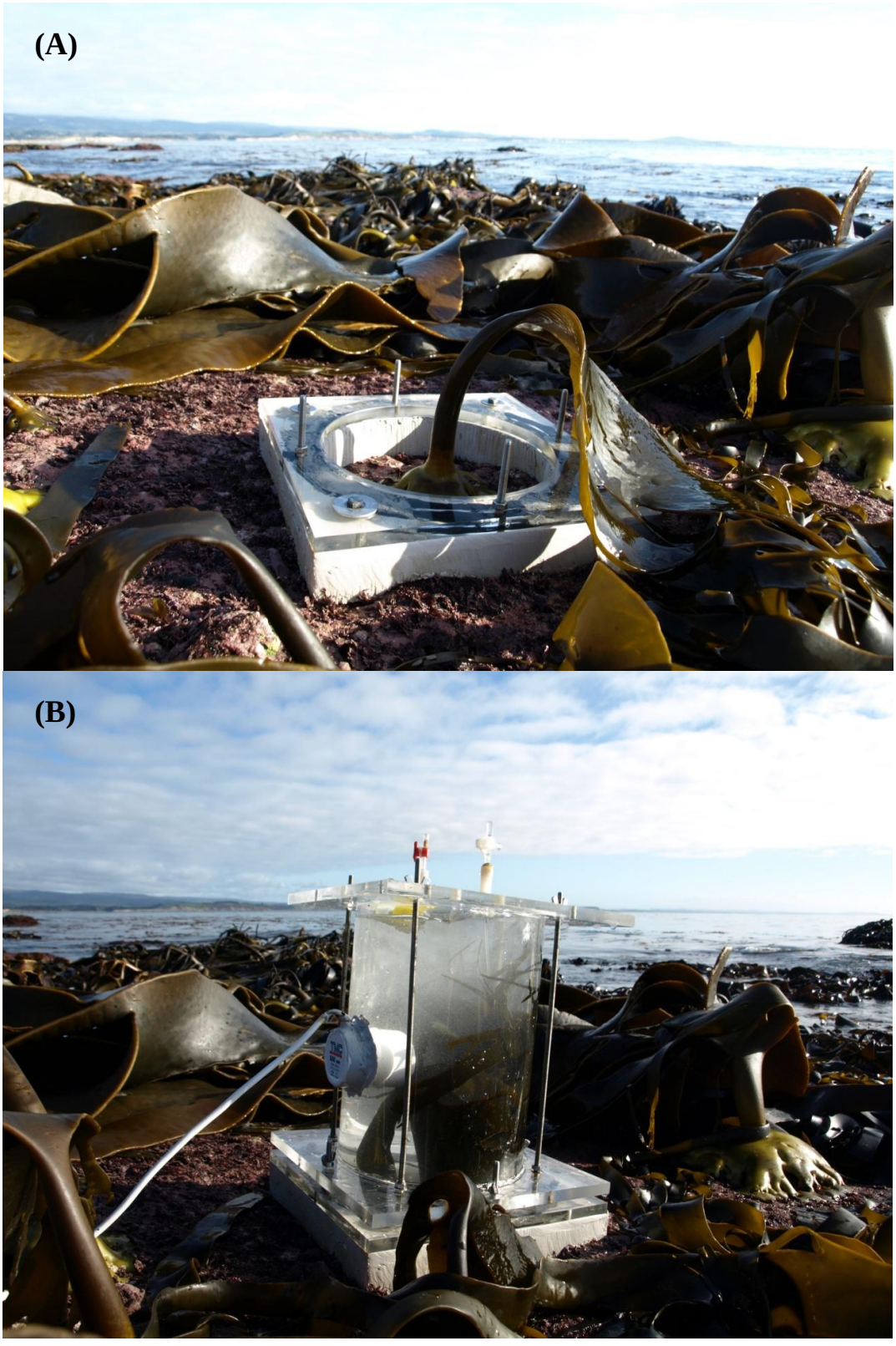

Figure 6.1. Photos showing the base plate surrounding a moderate sized *D. antarctica* thalli (A) and the plant inside a filled chamber (B).

6.3. Results

6.3.1. *Mid shore chronosequence of production*

Species cover and composition of the mid shore zone of North reef, Moeraki, had a large variation between removal and control plots over time (Fig. 6.2, Table 6.2). Over 12 months the control plots had relatively similar cover in the dominant species *Hormosira banksii*, *Corallina officinalis*, encrusting corallines and *Cystophora torulosa*. Algal diversity within the 3 replicate control plots ranged between 8-9 species over the 12 month period. The new minus *H. banksii* treatment had a slight increase in *C. officinalis* and a decline in *C. torulosa* over time. Furthermore, after 6 months *H. banksii* had started recruiting into these plots and had reached almost 40% cover by 12 months. Diversity within the new minus *H. banksii* treatments increased from an average of 6 species (directly after removal) to an average of 8 species (6 and 12 months after removal). The old minus *H. banksii* treatment showed very little variation in species composition over time, with very similar cover of the dominant species *H. banksii*, *C. officinalis* and encrusting corallines throughout the experiment. Diversity ranged between 5-6 species over the 12 months, with many of the species being found in very low densities compared to the dominant species.

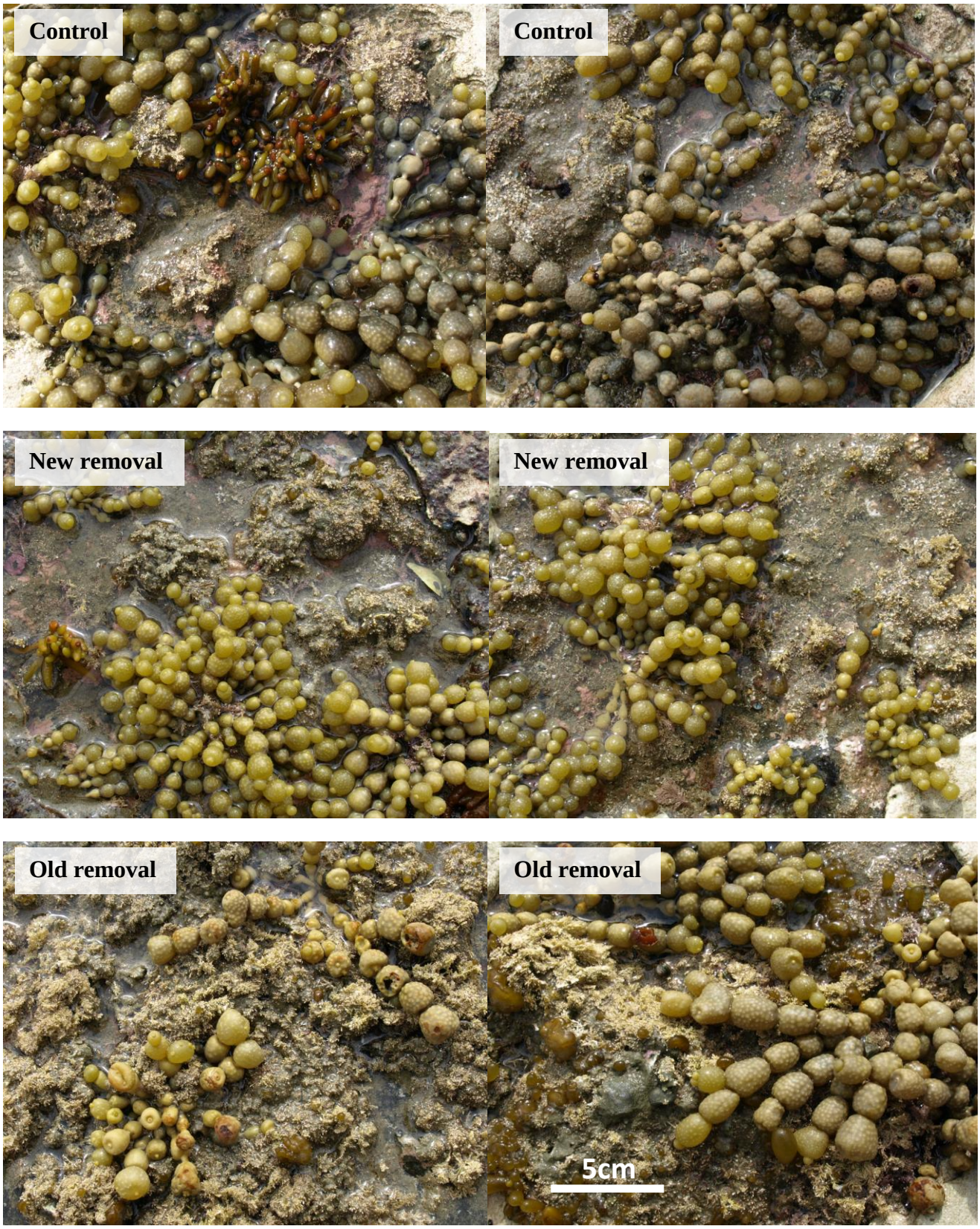

Figure 6.2. Photos showing the cover and composition of the *H. banksii* dominated assemblages in control, new removal (after 12 months) and old removal (after 72 months).

Table 6.2. Average species cover and abundance within incubation plots in the three treatments, control, old *H. banksii* removal and new *H. banksii* removal at 0, 6 and 12 months, since the start of the experiment.

Average percent cover	Control			Old removal			New removal		
	0	6	12	0	6	12	0	6	12
Hormosira banksii	78.3	84	86.7	33.3	31.7	25	0	9.3	36.7
Corallina officinalis	38.3	42	56.7	88.3	85	81.7	61.7	71.3	71.7
Encrusting coralline	46.7	43	26.7	7.7	4	6.7	21.7	13.3	13.3
Cystophora torulosa	11.7	9.5	7.3	0	0.3	0	15	2.3	3.3
Jania micrarthrodia	1	1	1	0.3	0	0	1	0	0
Splachnidium rugosum	8.3	5.5	3.3	0	0	0	0	0	1
Colpomenia bulosa	0.7	0.5	1	1.3	1.6	5.3	0	2	3
Champia novae-zelandiae	0.3	0.3	0.3	0	0	0	0	0.3	0
Ralfsia verrucosa	1	1	0	0	0	0	1.3	0.6	0.6
Adenocystis utricularis	0	0	0	0.3	2	2.3	0	2	0.3
Ulva spp	0	0	0	0	0.6	0	0	0	0
Haliptilon roseum	0	0	0	0	0	0	0.3	0	0

The loss of *H. banksii* had a major affect on the production of these mid shore assemblages (Fig. 6.3). The control *H. banksii* assemblage had much higher production than the old and new minus *H. banksii* treatments at high irradiance (>1500µmol m^{-2} s^{-1}). This was true for data standardised by both dry weight and reef area at 0 months and 6 months. There was also a major difference between the production of the old and new removal treatments at time zero (48 months for old minus *H. banksii*), with the new minus *H. banksii* treatments showing higher production. However, after 6 months the new minus and old minus *H. banksii* were similar when standardised by area and dry weight. At six months the new minus *H. banksii* showed a linear increase in production with irradiance, whereas the old minus *H. banksii* treatment changed from a photoinhibition curve to a saturation curve.

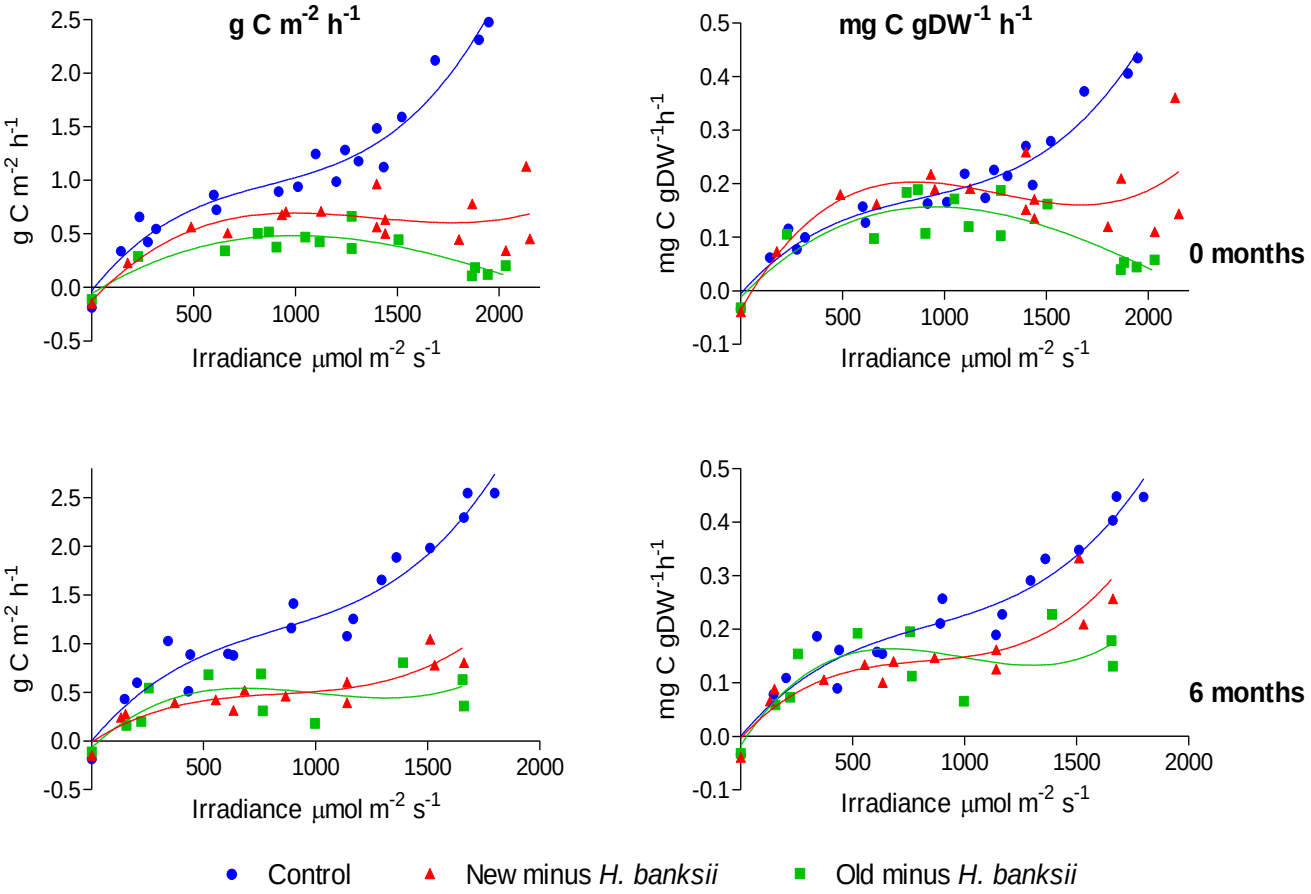

Figure 6.3. Primary production of *H. banksii* dominated assemblages in Moeraki and the effects of short term and long term canopy loss. Data are standardised by reef area (g C m^{-2} h^{-1}) and dry weight (mg C gDW^{-1} h^{-1}) at two intervals, 6 months apart (new removals started at 0 months).

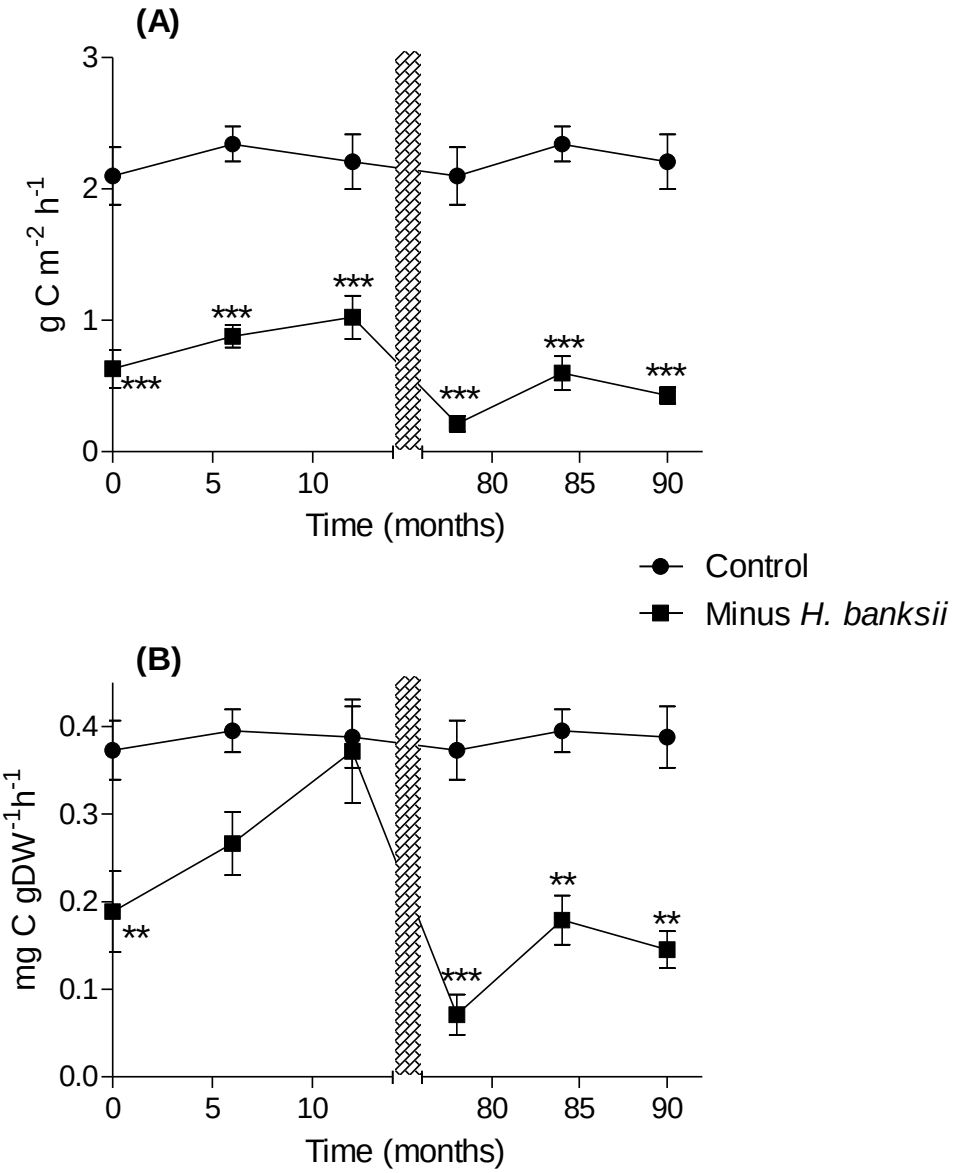

Figure 6.4. Effects of canopy removal on the recovery of primary production (±SE) over time, using new and old removal plots, North reef, Moeraki. Data are standardised by (A) reef area (g C m^{-2} h^{-1}) and (B) dry weight (mg C gDW^{-1} h^{-1}). Shaded bar indicates the change from new minus *H. banksii* treatments and old minus *H. banksii* treatments. Significant difference between control and removal shown by * (*, p < 0.05; **, p < 0.01; ***, p < 0.001).

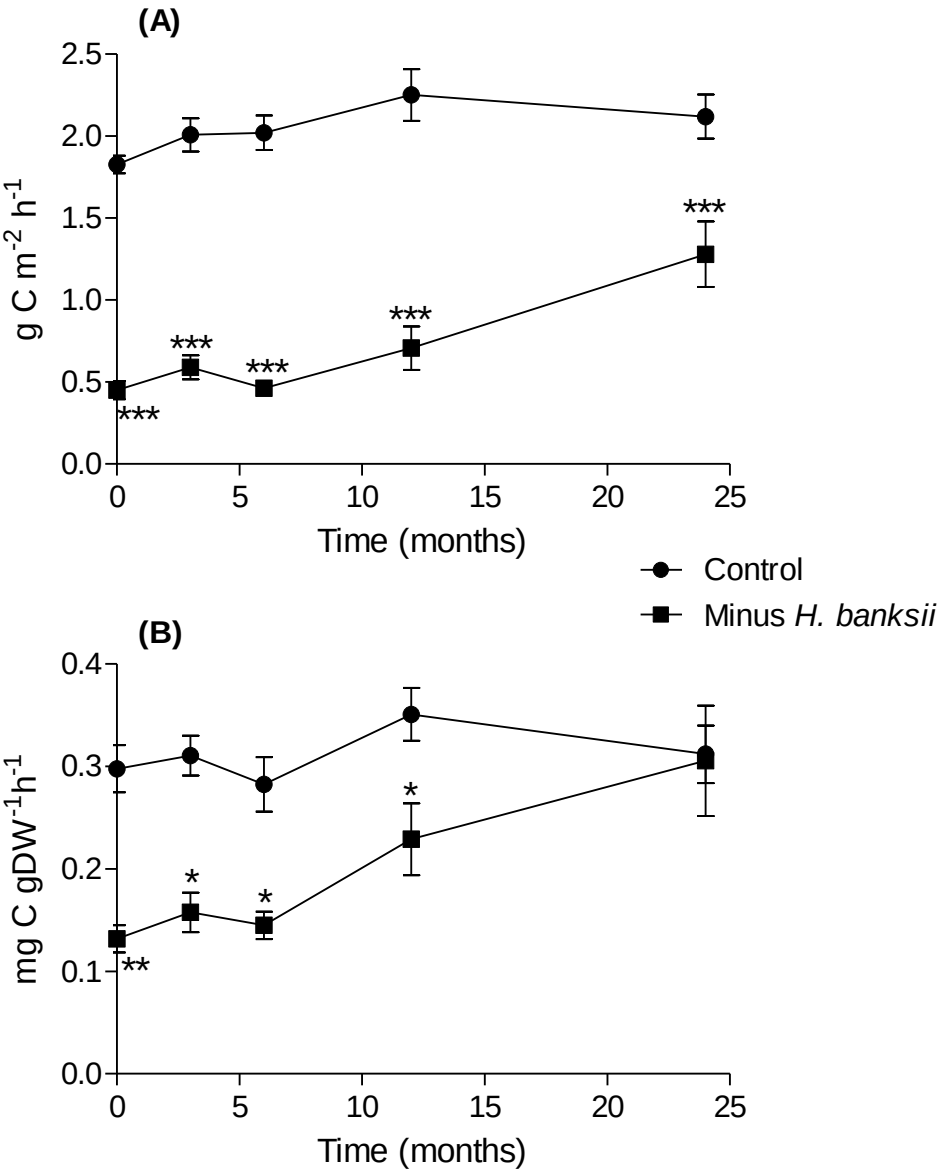

Figure 6.5. Effects of *H. banksii* canopy removal on recovery of primary production (±SE) over time, Wairepo reef, Kaikoura. Data are standardised by (A) reef area (g C m^{-2} h^{-1}) and (B) dry weight (mg C gDW^{-1} h^{-1}). Significance shown by * (*, p < 0.05; **, p < 0.01; ***, p < 0.001).

Change in primary production over time showed that after the initial disturbance there is a trend of recovery, but after approximately 5 years, production is much reduced in the removal treatment, regardless of standardisation (Fig. 6.4). Two-way ANOVA shows a significant effect of treatment ($F_{1,43}$ = 285, p < 0.0001) and time ($F_{5,43}$ = 2.5, p < 0.05), but no interaction when standardised by reef area. When analyzed by dry weight, a two-way ANOVA shows a significant effect of treatment ($F_{1,41}$ = 75, p <

0.0001) and time ($F_{5,41}$ = 4.8, p < 0.001). Also there is a significant interaction effect between treatment and time (treatment x time, $F_{5,41}$ = 4.1, p < 0.001). Bonferroni post-hoc tests also indicate a significant difference between control and minus *H. banksii*, standardised by reef area, at all periods after removal (0; t = 6.53, p < 0.001, 6; t = 5.73, p < 0.001, 12; t = 6.0, p < 0.001, 78; t = 8.4, p < 0.001, 84; t = 6.8, p < 0.001, 90; t = 8.8, p < 0.001). When standardised by dry weight, Bonferroni post-hoc tests also indicate a significant difference between control and minus *H. banksii*, at all periods after removal (0; t = 3.6, p < 0.01, 6; not significant, 12; not significant, 48; t = 5.9, p < 0.001, 54; t = 3.9, p < 0.01, 60; t = 5.3, p < 0.001). Although after 48 months the community had not recovered, at 12 months the new *H. banksii* removal plots were fairly close to control levels and when considered by dry weight, were not significantly different from controls at 6 and 12 months after removal.

Change in primary production over time at the Kaikoura site showed increasing primary production over time in the minus *H. banksii* treatment (Fig. 6.5). After two years, assemblage primary production after canopy removal had reached control levels when standardised by dry weight, and close to control when standardised by reef area. There was a significant effect of treatment on production (Two way ANOVA; $F_{1,41}$ =270, p < 0.0001) and time ($F_{4,41}$ = 6.5, p < 0.0001) per reef area. There was also a significant interaction effect between treatment and time ($F_{4,41}$ = 2.8, p < 0.05). When standardised by dry weight, there was a significant effect of treatment on production (Two way ANOVA; $F_{1,43}$ = 31.2, p < 0.0001) and time ($F_{4,43}$ = 4.1, p < 0.0001). Bonferroni post-hoc tests show a significant difference between the treatments standardised by reef area at 0 (t = 6.8, p < 0.001), 3 (t = 8.2, p < 0.001), 6 (t = 8.1, p < 0.001), 12 months (t = 8.9, p < 0.001), and 24 months (t = 4.8, p < 0.001). Bonferroni post-hoc tests show a significant difference between the treatments standardised by dry weight at 0 (t = 3.3, p < 0.01), 3 (t = 3.2, p < 0.05), 6 (t = 2.9, p < 0.05), 12 months (t = 2.7, p < 0.05), but not at 24 months. The increase in primary production over time in the Kaikoura treatments was also correlated with a recruitment of *H. banksii*, with cover reaching over 60% by two years. However, after 5 years, neither production nor canopy cover had recovered in the Moeraki plots.

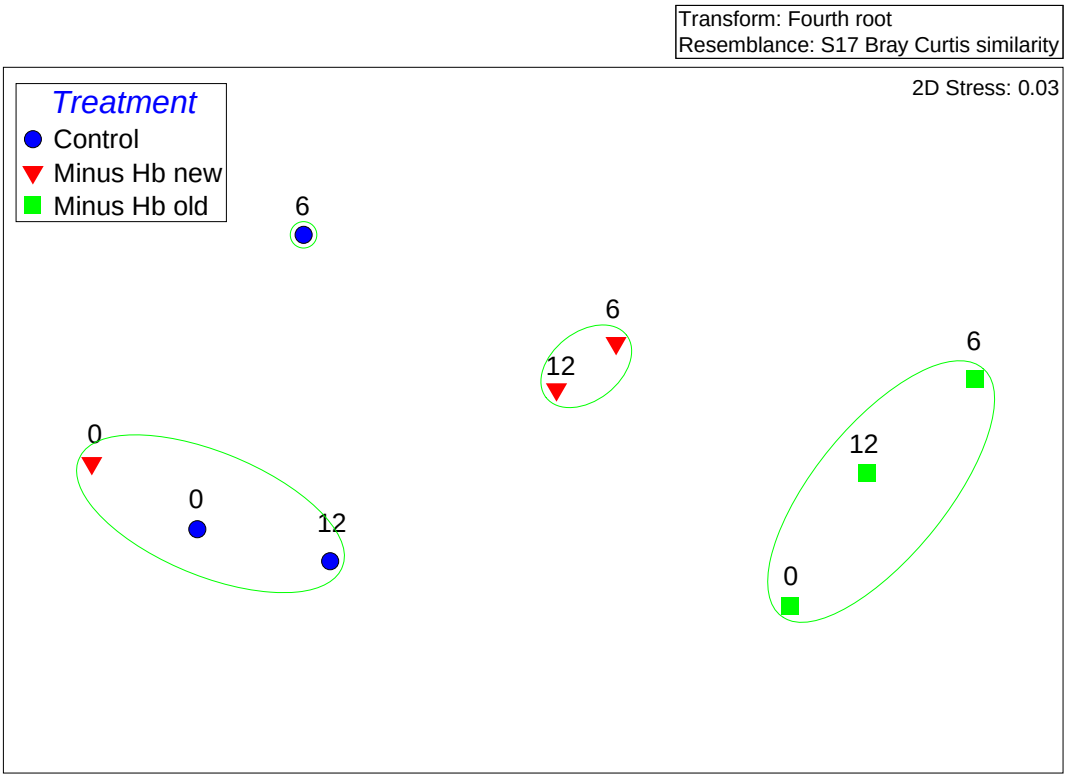

Figure 6.6. MDS plots of changing community composition in control, and chronosequence of canopy removal in *H. banksii* plots (Minus Hb) at Moeraki. Numbers above symbols indicate the number of months since the beginning of the experiment and circles indicate CLUSTER analysis of 80% similarity.

Multi-dimensional scaling plot indicated a large variation in assemblage structure in the removal treatments over time (Fig. 6.6). All three replicates of each treatment were averaged in order to visualize the trajectory of change. Although the control and the new removal treatment started out similar (grouped within 80% similarity, CLUSTER analysis), the new removal treatment diverged, with the community structure at 6 and 12 months grouping well away from controls at the same time. As time after removal increased, the community structure was increasingly different from the control communities. At 72 months the removal treatment was grouping well away from all the control plots. PERMANOVA analysis of community composition showed a significant difference between treatment ($F_{2,12}$ = 19.5, $p < 0.005$) and time ($F_{2,12}$ = 7.6, $p < 0.05$).

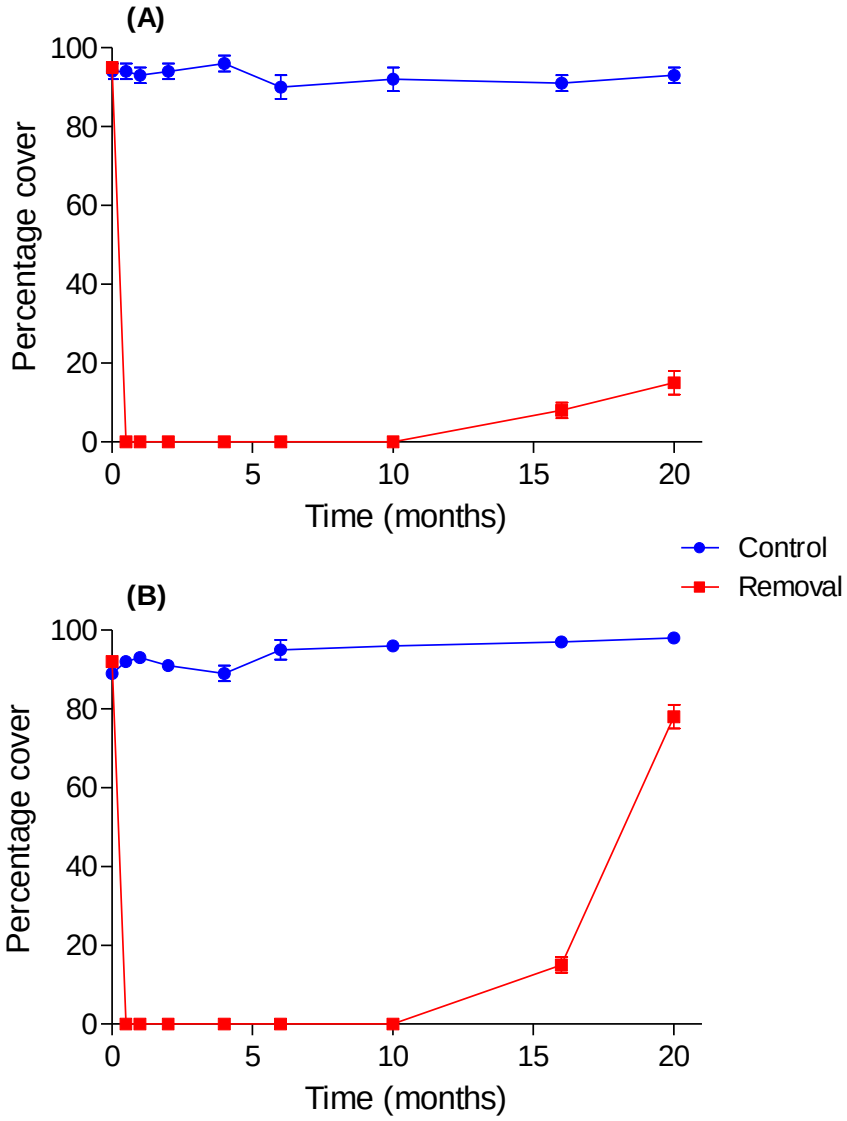

Figure 6.7. Percentage cover (±SE) of adult *H. banksii* in control and removal treatments at two sites (A) North reef, Moeraki, and (B) Wairepo, Kaikoura. Data from Lilley (2004).

Changing cover of the dominant canopy species in the original removal experiment revealed a very slow recovery of *H. banksii* once removed (Fig. 6.7). Furthermore, the Kaikoura site (Fig 6.7. B) had much greater recovery of *H. banksii* at 20 months than the Moeraki site (Fig. 6.7 A). After 20 months cover of *H. banksii* at Kaikoura was approaching 80%, compared to only 20% at Moeraki. Although the data only shows 20 months of data, cover of *H. banksii* at 60-72 months after removal showed that cover of *H. banksii* was only 25-30%, compared to 85% in the controls (Table 6.2).

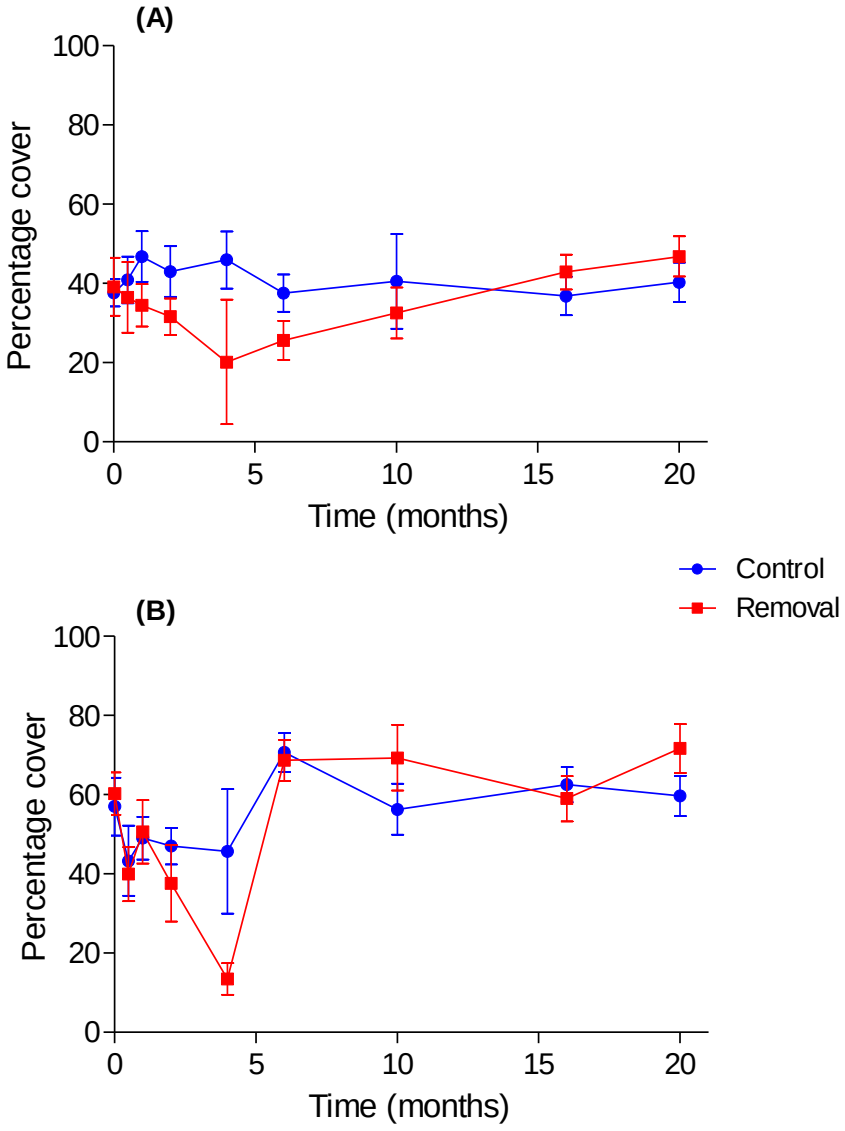

Figure 6.8. Percentage cover (±SE) of adult *Corallina officinalis* in control and removal treatments at two sites (A) North reef, Moeraki, and (B) Wairepo, Kaikoura. Data from Lilley (2004).

Cover of *C. officinalis* following the removal of the dominant canopy species *H. banksii* shifted significantly over time (Fig. 6.8). Initially after canopy removal, *C. officinalis* cover dropped in the removal treatments, but over time, it began to recover, and even exceed the cover of *C. officinalis* in the control plots. Although data were only recorded up to 20 months after removal, after 60-72 months cover of *C. officinalis* was between 81-88% compared to only 38-56% in the control treatment (Table 6.2).

6.3.2. *Low shore chronosequence of production*

Species cover in control plots had a *Durvillaea antarctica* canopy cover of 100% at both sampling intervals, and the cover of the remainder of the species stayed relatively constant (Fig. 6.9, Table 6.3). The new removal treatment had a 30% increase in the cover of coralline turf (predominantly *Haliptilon roseum*) over the six months, but an overall decline in algal diversity. Although the cover of several other species increased, there was no recruitment of *D. antarctica* after six months. In the old removal treatment *D. antarctica* cover increased, and coralline turf remained relatively constant (increased by only 0.3%). There was also a high species diversity, with 14 species occurring in relatively low abundance (6 species with less than 1% cover). In the old minus *D. antarctica* treatment there was a large variation in species diversity and cover between the sites, plots were dominated by *Cystophora torulosa*, *Undaria pinnatifida*, *C. officinialis* and *Xiphophora gladiata*, with only a small amount of *D. antarctica* (less than 11%). Overall diversity in the old minus *D. antarctica* plots was very high, and was higher than the diversity of the control plots. In the old minus *D. antarctica* treatment no single species dominated a plot, and the canopy was often comprised of several species.

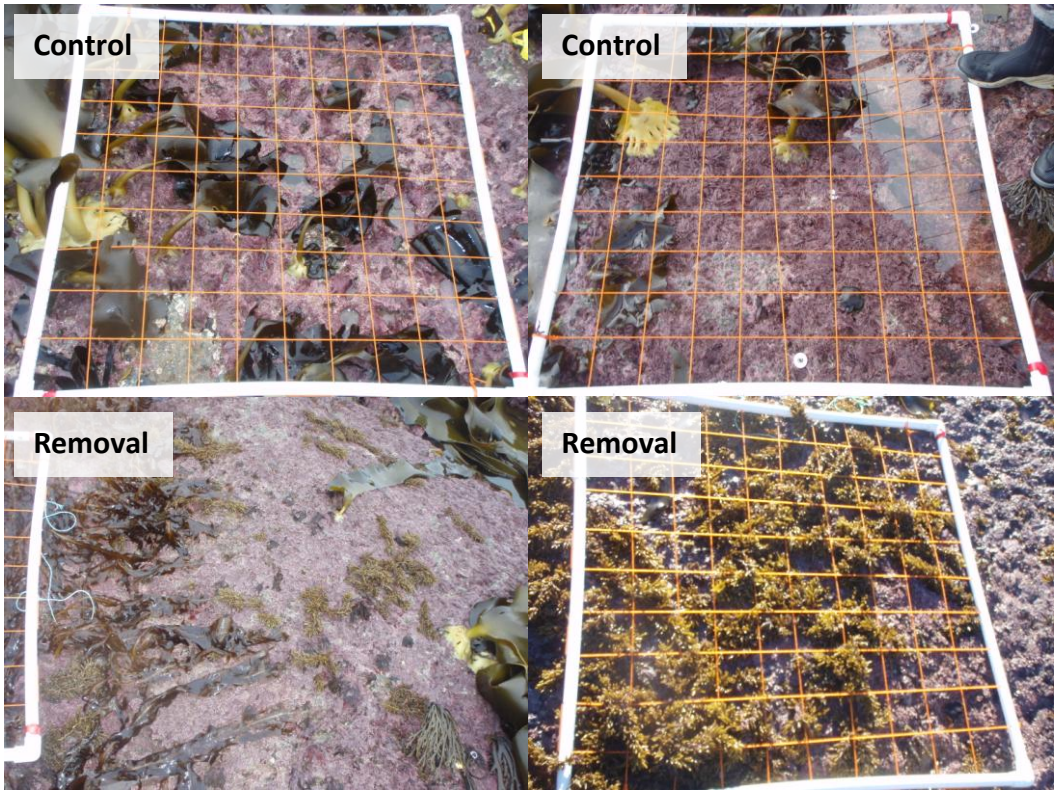

Figure 6.9. Photos showing the cover and composition of the subcanopy macroalgal assemblage in control, and *D. antarctica* removal. Quadrat within photos was 1x1 m.

Table 6.3. Average species cover and abundance within incubation plots in the three treatment control, old *H. banksii* removal, and new *H. banksii* removal at 0, and 6 months since the start of the experiment.

Average percent cover	Control		Old removal		New removal	
	0	6	0	6	0	6
Durvillaea antarctica	100	100	6.7	10.3	0	0
Haliptilon roseum	30	30	41.7	42	30	56.7
Jania micrarthrodia	7	8	3.3	3.3	5.7	14
Encrusting coralline	43.3	41	33.3	31.7	70	16.7
Cystophora torulosa	0.3	0.3	50.3	55.7	0.7	0
Xiphophora gladiata	0.7	0.7	6.7	6.7	0.3	1.3
Lophothamnion hirtum	0.3	0.3	13.3	6.6	0.67	8.6
Chaetomorpha coliformis	0.5	1	0	0.3	0.7	0
Codium dimorphum	0.7	0.7	0	0	0.7	0.6
Gigartina decipiens	0.7	1	10	12.3	10	1.6
Halopteris virgata	10	7.3	0.3	0.6	0	7.3
Cystophora retroflexa	0	0	0.3	0.3	0	0
Undaria pinnatifida	0	0	30	38.3	0	0
Hormosira banksii	4	0	3.3	2	0	0
Colpomenia sinuosa	0	0	0.3	0	0	0
Laurencia thyrsifera	0	0	0.3	0	0	0
Polysiphonia strictissima	0	0	0.6	0.6	0	0

Primary production in the intact, *D. antarctica* assemblages was much higher than both the new or old minus *D. antarctica* treatments regardless of the unit of standardisation (Fig. 6.10). The *D. antarctica* assemblage showed a very extreme increase in primary production at irradiances above 1500 µmol m^{-2} s^{-1}. The old minus *D. antarctica* treatment was more productive than the new removal treatment when standardised by reef area, but not by dry weight. There was very little difference in production in all three treatments between the sampling periods, although the old minus *D. antarctica* treatment was slightly more productive at 6 months, and the new minus *D. antarctica* was slightly less productive at 6 months.

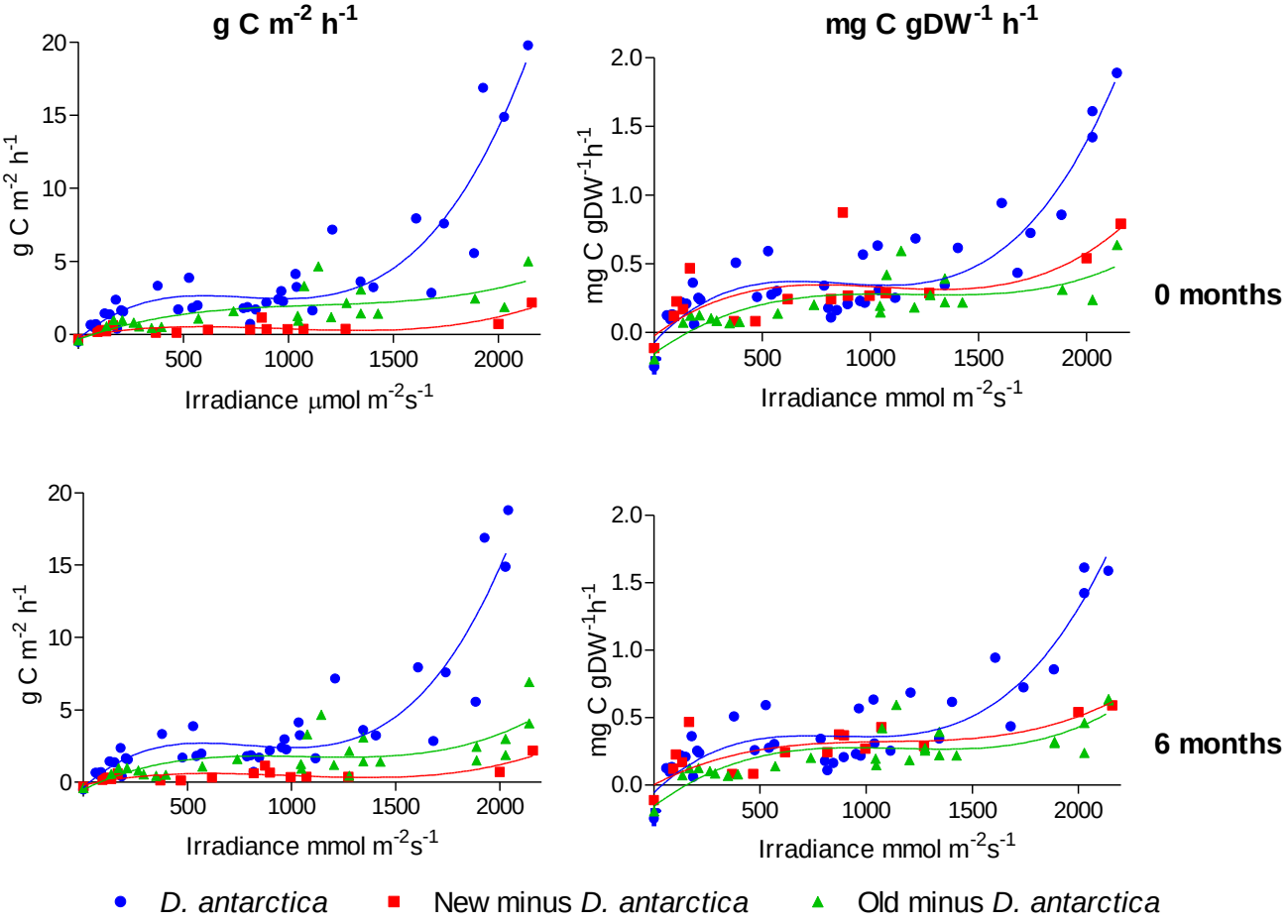

Figure 6.10. Primary production of *D. antarctica* assemblages and the effects of canopy loss on assemblage production. Data are standardised by (A) reef area (g C m^{-2} h^{-1}) and (B) dry weight (mg C gDW^{-1} h^{-1}) and show production at two intervals 6 months apart (new removals started at 0 months).

The species composition and cover of assemblages dominated by *U. pinnatifida* indicated a relatively diverse assemblage with high average cover of a number of species, including 80% *U. pinnatifida*, 25% *C. torulosa*, 50% *C. officinalis* and 15% *Ballia hirsuta* (Fig. 6.11). *U. pinnatifida* formed the majority of the assemblage, but *C. officinalis*, *C. torulosa*, *X. gladiata*, and *B. hirsuta* had relatively high cover as well. The production of the *U. pinnatifida* assemblage was similar per area, and higher per dry weight than *D. antarctica* throughout most of the irradiance range (Fig. 6.12). However, at high irradiance *D. antarctica* was much more productive than *U. pinnatifida* assemblages, regardless of standardisation. The *U. pinnatifida* assemblage had more of a saturation relationship with irradiance, with no large rise in production as was seen in *D. antarctica*.

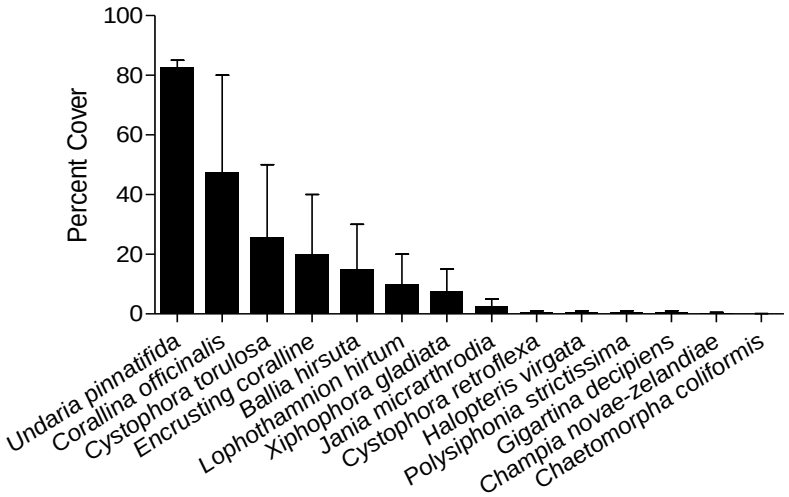

Figure 6.11. Species composition and percentage cover (±SE) in plots dominated by *U. pinnatifida*.

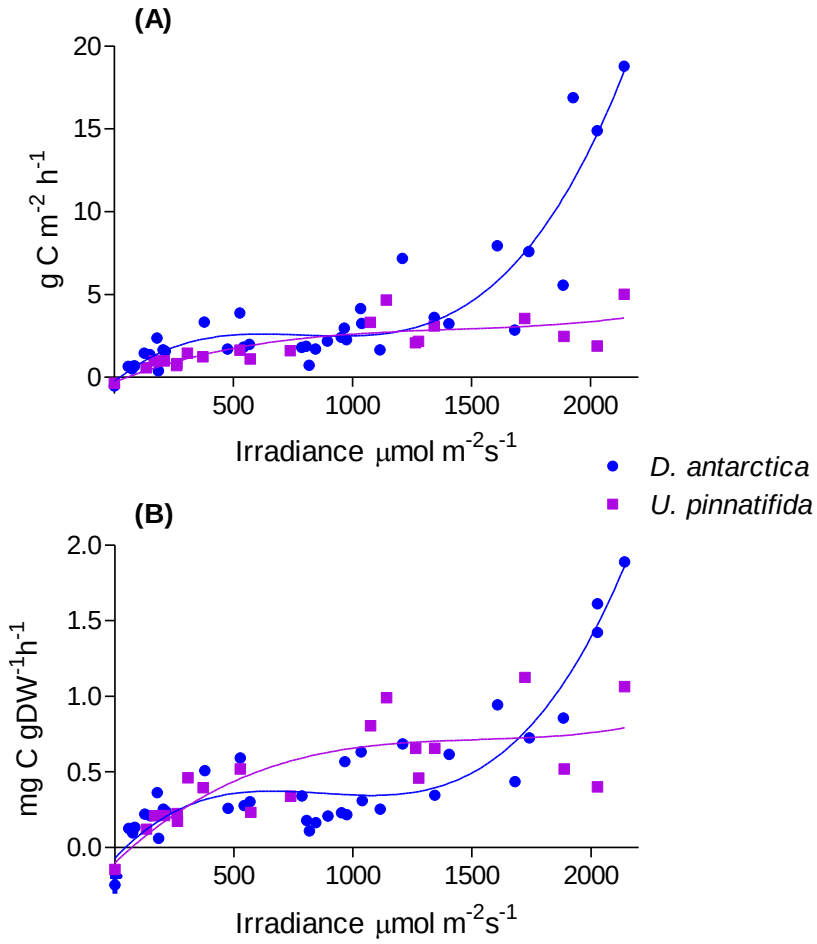

Figure 6.12. Production vs. irradiance for the native *D. antarctica* assemblage and the invasive *U. pinnatifida* dominated assemblage. Data are standardised by (A) reef area (g C m^{-2} h^{-1}) and (B) dry weight (mg C gDW^{-1} h^{-1}).

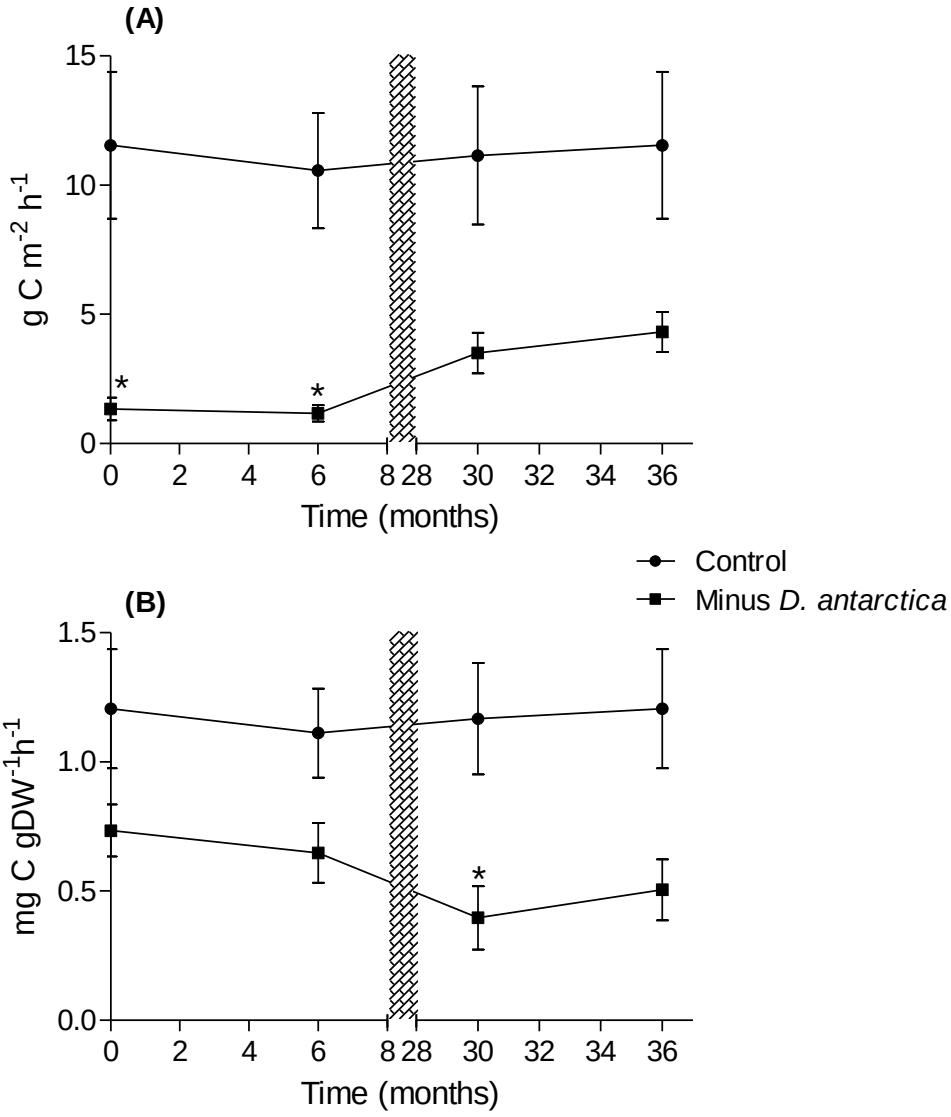

Figure 6.13. Primary production (±SE) of *D. antarctica* dominated assemblages and the effects of canopy removal on production over time. Data are standardised by (A) reef area (g C m^{-2} h^{-1}) and (B) dry weight (mg C gDW^{-1} h^{-1}). Shaded bar indicates the change from new minus *D. antarctica* treatments and old minus *D. antarctica* treatments. Significant difference between control and removal treatments shown by * (*, $p < 0.05$).

Change in primary production over time in the removal treatment indicated an initial fall in production, followed by a slight improvement (Fig. 6.13). After 3 years production was increasing towards control, but even after 42 months, the control was still more productive. However, when standardised by dry weight, production was very close to control after 42 months. Two-way ANOVA shows a significant effect of treatment on primary production ($F_{1,33}$ = 30, $p < 0.0001$), but no significant effect of time or interaction effect when standardised by reef area. Bonferroni post-hoc tests showed

significant differences between control and canopy loss at time 0 (t = 3.1, p < 0.05), and 6 months (t = 2.8, p < 0.05). When standardised by dry weight, treatment had a significant effect on production ($F_{1,32}$ = 19.9, p < 0.0001), but again there was no effect of time, and no interaction. Bonferroni post-hoc tests show significant differences between control and canopy loss, only at 36 months (t = 2.8, p < 0.05). Although post-hoc test analyses do not show significant differences, there was still a trend of lower production in the removal treatments regardless of standardisation unit.

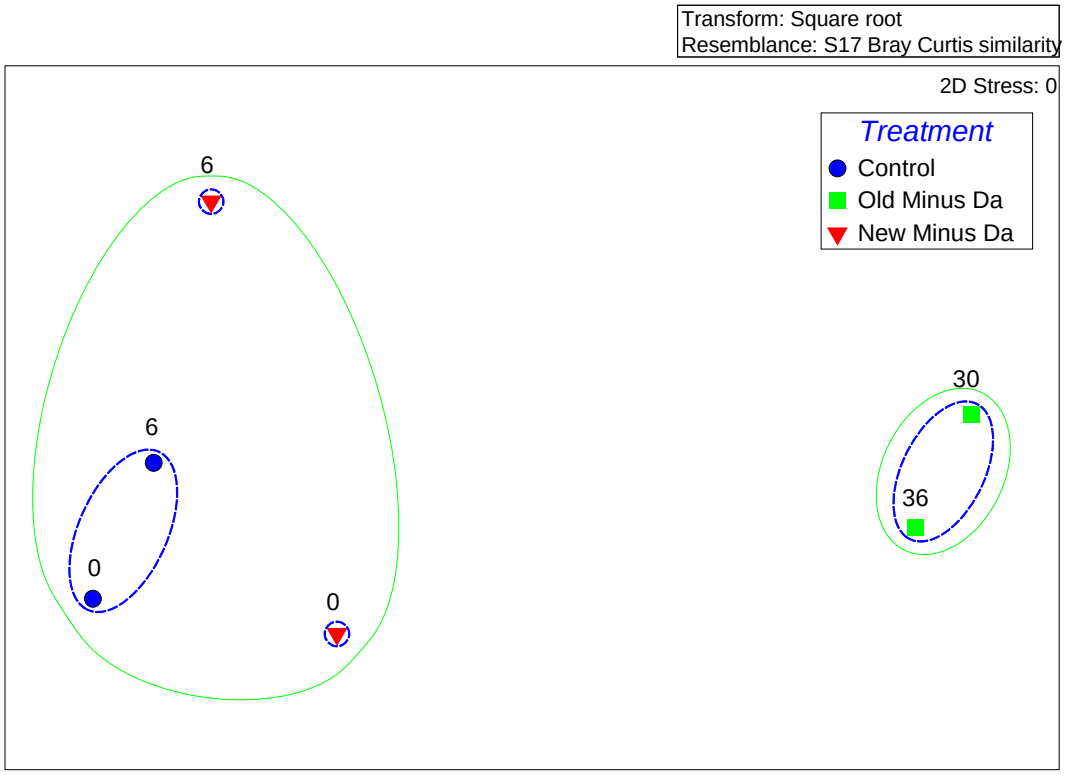

Figure 6.14. MDS plots of changing community composition in control, and chronosequence of canopy removal in *D. antarctica* plots (minus Da) at Moeraki. Numbers above symbols indicate the number of months since the beginning of the removal experiments and circles indicate CLUSTER analysis 80% (blue circles) and 60% (green circles) similarity.

Multi-dimensional scaling plots of community composition show an obvious separation between treatments (Fig. 6.14). All three replicates of each treatment were averaged in order to visualize the trajectory of change. Although control and new removal treatments were similar at time zero (grouped within 60% similarity, CLUSTER analysis), as time since removal progressed, the old removal treatment moved further away in multi-dimensional space from the controls. This represented the shifting

dominance of assemblages from *D. antarctica* to *U. pinnatifida* and *C. torulosa* in many cases. Furthermore, there was much wider variation in the new removal treatments compared to the control treatments, which changed very little over 6 months. PERMANOVA analysis showed significant differences between treatment ($F_{2,52}$ = 14.3, p < 0.0001), but no significant effect of time.

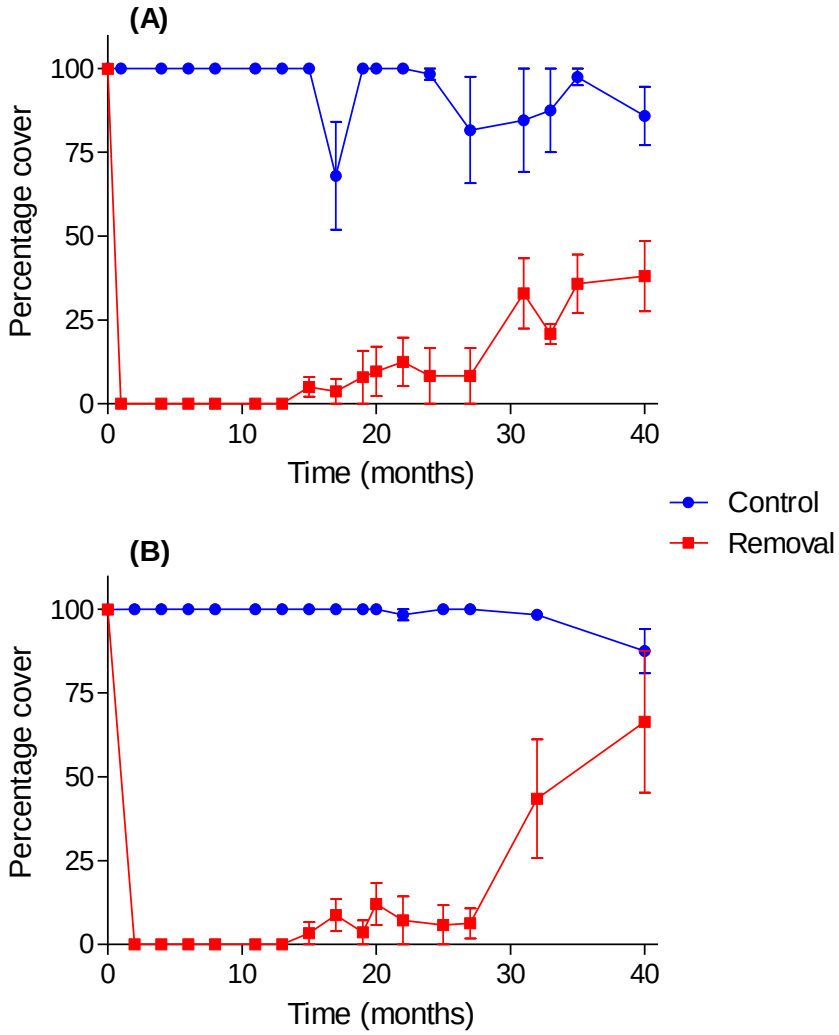

Figure 6.15. Percentage cover (±SE) of adult *D. antarctica* in control and removal treatment at two sites (A) North reef, Moeraki, and (B) Oaro, Kaikoura.

Changing cover of adult *D. antarctica* plants over time indicated a large variation between treatments and sites (Fig. 6.15). The recovery from the experimental removals was different between the sites, with the Oaro site showing greater recovery of adult *D. antarctica* canopy cover at 40 months. Two-way ANOVA with repeated measures analysis showed that at both sites there was a significant effect of treatment (Moeraki, $F_{1,68}$ = 530, p < 0.0001; Oaro, $F_{1,60}$ = 643.5, p < 0.0001) and time (Moeraki, $F_{17,68}$ = 8.1, p

< 0.0001: $F_{15,60}$ = 13.7, p < 0.0001). There was also a significant interaction between treatment and time (treatment x time; Moeraki, $F_{17,68}$ = 17.0, p < 0.0001; Oaro, $F_{15,60}$ = 16.9, p < 0.0001). Bonferroni post-hoc tests show a significant difference between percent cover after 40 months at Moeraki (t = 5.0, p < 0.001), but not at Oaro, indicating high levels of *D. antarctica* recovery at this site.

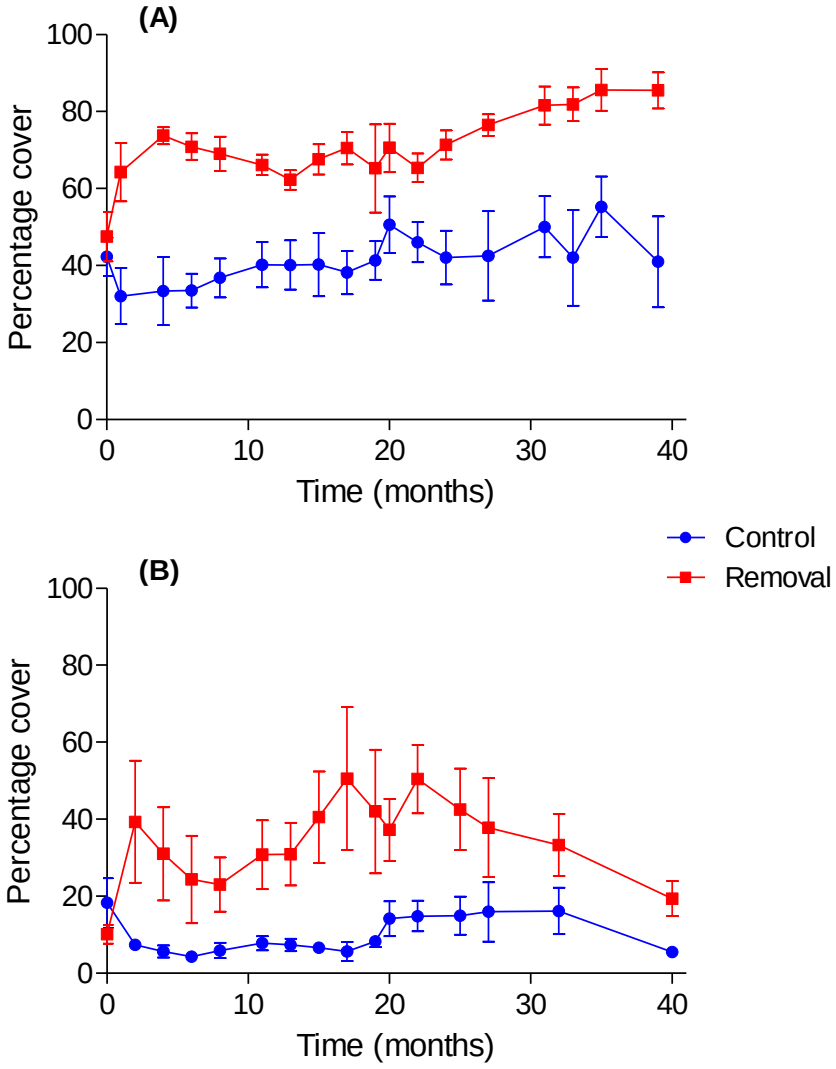

Figure 6.16. Percentage cover (±SE) of coralline turf in control and removal treatment at two sites (A) North reef, Moeraki, and (B) Oaro, Kaikoura.

The removal of *D. antarctica* from the plots in Moeraki and Kaikoura had a positive effect on the cover of coralline turf species (predominantly *Haliptilon roseum* in Moeraki and *Corallina officinalis* in Kaikoura; Fig 6.1). Within four months the coralline turf cover increased by approximately 40% in the removal treatment at the Moeraki site. After 2 months of canopy loss, coralline cover at the Kaikoura site had increased by 20-

30%. A major difference between the two sites was the two-fold higher cover of coralline turf in the Moeraki treatments (control and removal), as well as less variability in turf cover over time. The Kaikoura site had a large degree of variability over time, and towards 40 months there was a large fall in coralline turf cover across both treatments. Interestingly, this decrease in coralline turf cover at this time was associated with an increase in adult *D. antarctica* recruitment at 40 months in the removal treatment at the Kaikoura site (Fig. 6.15).

Table 6.4. Average (±SE) and maximum low intertidal temperature for quarterly periods from June 08 till June 09 at Oaro reef, Kaikoura and north reef Moeraki.

	Oaro, Kaikoura		North reef, Moeraki	
Date	Average Temp ˚C	Maximum Temp ˚C	Average Temp ˚C	Maximum Temp ˚C
June-Aug 08	8.35 (0.008)	13.7	8.49 (0.009)	17.07
Sep-Dec08	11.44 (0.02)	29.85	11.22 (0.014)	25.67
Jan-March 09	16.26 (0.012)	35.44	15.75 (0.02)	27.46
March-June 09	12.8 (0.013)	21.74	12.79 (0.02)	17.987

Average temperature data for Moeraki and Kaikoura indicate very similar temperatures throughout the year, but temperature was half a degree higher during January to March at the Kaikoura site (Table 6.4). Although temperature was slightly higher in Moeraki during winter, Kaikoura showed higher temperatures in the Sep-Dec quarter. Average temperatures were almost identical during the March-June 2009 quarter. Maximum temperatures show very different results, with Oaro showing a 8 degree higher maximum during Jan-March. Although Moeraki shows a higher maximum during June-Aug 2008, Kaikoura shows a higher maximum temperature in all other quarters.

6.4. Discussion

6.4.1. *Effects of canopy disturbance on assemblage composition and primary production*

Canopy forming macroalgae provide a suite of services to marine intertidal communities, including primary production (Mann 1973) and amelioration of physical stress to sub-canopy flora and fauna (Bertness et al. 1999; Lilley & Schiel 2006). Besides the well documented effects of canopy loss on associated assemblages, the loss of macroalgal canopy also causes a major drop in the potential primary production output of the assemblage. Furthermore, studies have shown that following major disturbances, the recovery of a macroalgal assemblage can take several years (Underwood 1998; Underwood 1999; Lilley & Schiel 2006), and this study shows that until the canopy has recovered, primary production levels are unlikely to reach those of the pre-disturbed assemblage. In fact, primary production after the loss of canopy species is only a small proportion of production when the canopy is present. Furthermore, at the more southerly location studied (Moeraki), the recovery of canopy species back to control levels occurred very slowly, and in certain cases the assemblage remained significantly different from what it previously was 7.5 years after canopy removal. This has major consequences for how macroalgal assemblages may respond to major disturbances and the primary production of these assemblages during the interim recovery.

In the *Hormosira banksii* dominated assemblage, its loss had lasting effects on primary production at both Kaikoura and Moeraki. However, the loss of canopy from Moeraki assemblages and its inability to recover to its pre-disturbed state caused a lasting change in community composition and, consequently, significantly lower production. However, at Kaikoura, production and cover of *H. banksii* had recovered towards control levels after 2 years. The loss of *H. banksii* from Moeraki assemblages resulted in a switch to coralline turf dominated communities, which has thus far lasted 7.5 years. In the *Durvillaea antarctica* assemblages, there was a greater variation in the outcomes of canopy removal, and several replicate plots recovered in different ways, or in some cases, not at all. At Oaro (Kaikoura), all removal treatments have recovered *D. antarctica* canopies at levels similar to those of the controls after 42 months. However, the Moeraki removal treatment remained significantly different, and each replicate plot showed a very different community. One replicate was almost completely dominated by *Cystophora torulosa*, while another is dominated by turf and a matrix of *C. torulosa*, *Xiphophora gladiata* and *Undaria pinnatifida*, while the other although gaining more *D. antarctica*

cover, is still mainly turf dominated. Although there is significant cover of canopy fucoids, primary production was still significantly lower than the *D. antarctica* dominated controls 3 years after canopy loss.

The timing of disturbance could be a significant factor determining the recovery of these assemblages. Many of the fucoid species present on New Zealand reefs have significant variation in their reproductive season (Taylor 2002; Dunmore 2006). For example *D. antarctica*, is reproductively active during autumn and winter, whereas *C. torulosa* is reproductive in spring and summer (Dunmore 2006). Although there are differences in community composition when disturbed in various seasons (Schiel 2006), the canopy of *D. antarctica* has been slow to recover regardless of the season removed (Schiel, unpublished data). Therefore, the reasons for the lack of recovery are more complicated, and potentially involve a facilitative role of the adult *D. antarctica* canopy on its juveniles. Another unforeseen change in the removal treatments was the recruitment of the invasive kelp *Undaria pinnatifida*, which had been previously unreported on this reef, although present in a nearby harbour (Thompson 2004). The invasion of this exotic species could have potentially influenced the ability of native assemblages to recover. Gametophytes of *U. pinnatifida* remain dormant during the summer months and plants grow prolifically from late autumn to early summer (Thompson 2004). The summer dormant stage may allow other fucoid species to recruit and gain ascendancy. It is possible that the prolific growth stage of this species could have influenced the recruitment of *D. antarctica* during its reproductive months. Despite the fast growth and high production of *U. pinnatifida*, on a per area basis, it is less productive than *D. antarctica* at high irradiance. Regardless of the mechanisms affecting the recruitment and recovery of *D. antarctica*, its loss has significant consequences to the production of these ecosystems.

Invasion of the non-native laminarian *U. pinnatifida* appears to be disturbance mediated process in this system. The loss of the robust *D. antarctica* canopy enables *U. pinnatifida* to establish itself within these low intertidal communities. *D. antarctica* has a major controlling role on the subcanopy community through its 'whiplash' effect, which can severely stunt the growth of subcanopy algae (Santelices et al. 1980; Taylor & Schiel 2005). Species diversity is expected to decrease the invasibility of biological systems due to more complete utilisation of resources (Stachowicz et al. 1999). This study indicates that the loss of one species can alter the system enough to change its invasibility. This gives further impetus for the 'key' species debate in these fucoid dominated assemblages

(Schiel 2006), and shows the reliance of these ecosystems on canopy forming fucoids. Although a variety of macroalgal species recruited into the removal treatments, these species (i.e., *C. torulosa*) were not able to exclude *U. pinnatifida* as *D. antarctica* did. Invasive species are touted as one of the leading causes of biodiversity loss (Wilcove et al. 1998) and alteration of ecosystem function (Stachowicz et al. 1999). This study indicates that invasion by *U. pinnatifida* causeed a significant fall in primary production compared to the native *D. antarctica* community, but due to its annual life history, may be unable to completely dominate these intertidal assemblages. It appears that this species keys into free space, and although its growth is prolific for part of the year, it dies off annually, potentially allowing native fucoids to recruit. This suggests that although this species may slow the recovery of native assemblages, it may not cause a prolonged shift in community structure.

The inability of disturbed fucoid assemblages to recover to control levels of canopy cover is concerning for the overall function of these assemblages. The large loss of primary production in the turf dominated assemblages suggests that these assemblages are significantly altered in both composition and function. The most likely explanation for the persistent loss of *H. banksii* cover is the interaction between recruiting fucoids and coralline turf (Lilley & Schiel 2006). Once released from competition with the canopy, turf forming species are able to grow prolifically, and this growth may affect the ability of the fucoid zygotes to find suitable bare space to colonize (Airoldi & Cinelli 1997; Airoldi 1998; Connell 2005). However, at the Kaikoura site, once the canopy was removed the coralline turf was subject to significant bleaching and burn-off (Lilley & Schiel 2006). It is also likely that a similar interaction may be occurring in the *D. antarctica* assemblages, where the removal of the canopy frees the turf from whiplash disturbance and increases light levels. The increase in cover and length of calcareous turf fronds may inhibit the settlement of many fucoids. However, unlike fucoid algae, *U. pinnatifida*, is able to recruit into patches dominated by coralline turf (Thompson 2004). Variation in temperatures and environmental conditions between the two sites may be responsible for differences in the relationship between fucoid and coralline turf. In particular, turf bleaching was observed to be much more common in the Kaikoura experiments (Lilley & Schiel 2006). Bleaching often occurs due to the combined effects of excess irradiance (UV and PAR) and temperature (Yellowlees & Warner 2003). Furthermore, cover of coralline algae increased significantly, and was able to persist at Moeraki, whereas Kaikoura showed greater fluctuations of coralline cover. The higher

temperature at the northerly Kaikoura site during summer may account for the variation in turf interactions at each site, and may increase the bare space available for fucoid recruits.

Although referring to these disturbed patches as an 'alternative stable state' may be a overstatement, these assemblages fill some of the criteria for a system which has been perturbed and remained changed (May 1977; Suding et al. 2004). Successional models of recovery suggest that once the abiotic conditions have been restored and a 'seed bank' persists, then communities will recover along their natural trajectory of succession (Suding et al. 2004). However, in this example, the abiotic state has presumably been restored, failing a major shift in climate, and a propagule bank is present, yet the assemblages still remain changed for up to 7.5 years after disturbance. It could be argued that the time allowed for full recovery has not been sufficiently long, yet very similar assemblages on the Kaikoura reef, approximately 400 kilometres away have recovered within 2 years for *H. banksii* and 3 years for *D. antarctica*. In this example, the size of the perturbation was large enough to shift the state of the assemblage, and although natural conditions have been restored, the system has not returned to the 'natural stable state.' It has been suggested that the mechanism by which the community is changed is not necessarily the mechanism which will shift the community back (Gunderson 2000; Suding et al. 2004). It is likely that a timely burn-off of the coralline turf, coupled with a good recruitment of *H. banksii* may tip the balance back in favour of the fucoid. However, given major shifts in abiotic conditions due to human disturbance, the assemblages may be influenced by a variety of other unforeseen factors which have not been reported. Large land-use changes in the terrestrial region (mainly intensification of livestock farming) may be altering the nutrient and sediment regimes, and could be subsequently altering the dynamics between turfs and fucoids. It has been shown that sediments increase the spatial dominance of these articulated coralline turfs (Airoldi & Virgilio 1998; Connell 2005) and this change has been associated with the concomitant decrease in canopy cover of fucoid algae (Airoldi & Cinelli 1997; Airoldi 1998; Connell 2005; Hurley 2009). Although higher temperatures may be causing coralline turf burn-off in the northerly Kaikoura site (Lilley & Schiel 2006), the lower temperatures, and potentially high input of sediments may be favourable for turf assemblages at the southern localities (Fig. 6.17). Furthermore, increasing frequency and intensity of waves (Trenberth 2005) and differences in exposure levels of the two sites may be affecting the settlement and attachment of zygotes (Taylor et al. 2010). Therefore, large disturbances

of fucoid canopies have the potential to become a common feature of southern reefs and could lead to a proliferation of coralline turf dominated zones. The low primary production potential of these calcifying algae (Littler & Arnold 1982) could have potentially devastating consequences on the surrounding ecosystems, and would represent a substantial loss of ecosystem function.

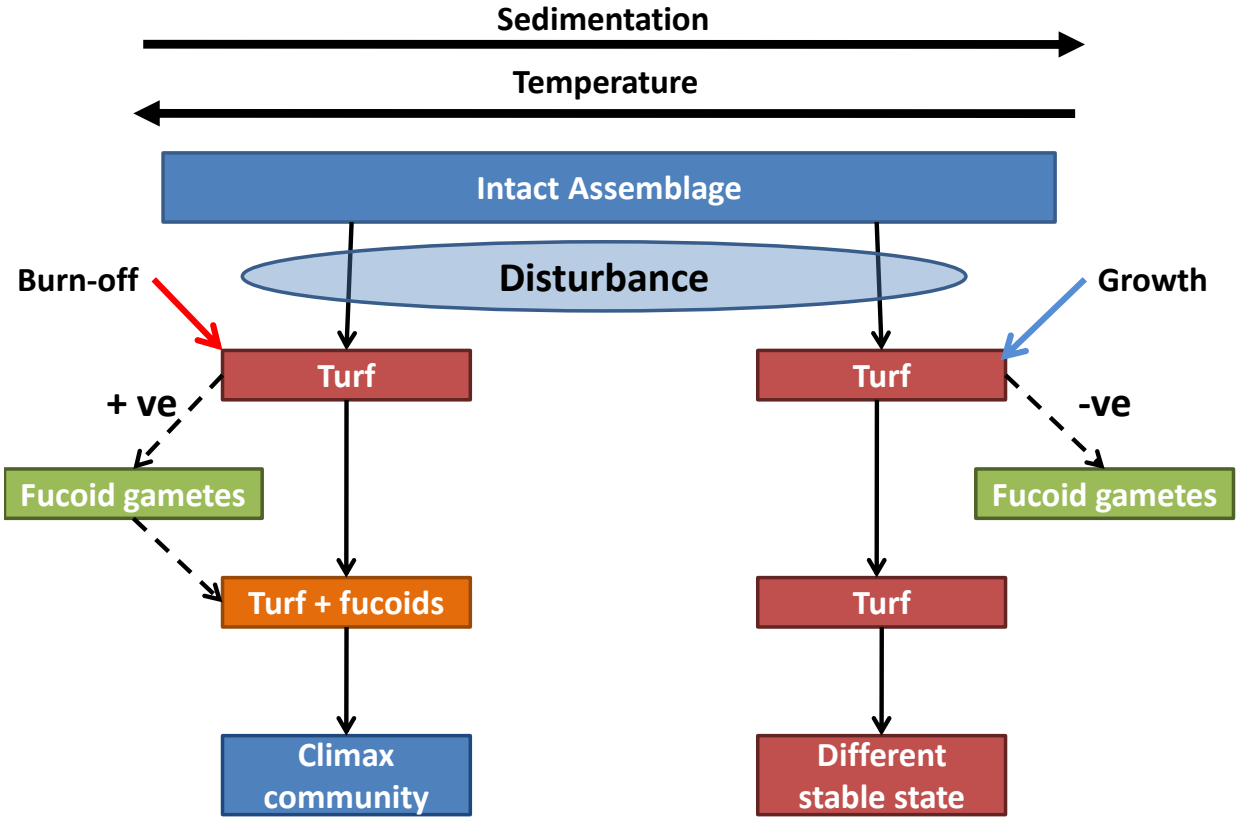

Figure 6.17. Flow chart indicating the effects of canopy loss on the trajectory of recovery. Chart shows the effects of canopy removal at two ends of a temperature or sedimentation gradient.

6.4.2. *Effects of multiple stressors on macroalgal assemblages*

Ecosystems are becoming more frequently subjected to multiple stressors (Crain et al. 2008; Schiel 2009), the effects of which are less well understood than individual stressors (Paine et al. 1998). In these intertidal macroalgal systems, canopy disturbance is a common occurrence, but due to increased nutrient and sediment loading, the effects of canopy disturbance may be exacerbated. The effects of multiple stressors fall into three

categories; 1) additive, i.e., the effects of each stressor 'A' and 'B' are the same in combination as they are alone (stress = A + B); 2) synergistic, i.e., the combination of the two stressors causes a reduced effect (stress < A + B); and 3) antagonistic, i.e., the combination of the two stressors causes an increased effect (stress > A + B; Folt et al. 1999; Crain et al. 2008). Stress is typically measured as some form of physiological response; however, in this example, the effects of multiple stressors are manifested in an alteration of community structure, and consequently primary production. Therefore, understanding whether the effects of canopy disturbance and sedimentation/nutrient enrichment are additive, synergistic or antagonistic is difficult. Also, canopy disturbance is the only 'known' stressor tested in this study and although sedimentation may play a significant role on these reefs, many other stressors may be impacting these systems, including; increasing wave stress, increasing ocean temperatures, and increased UV radiation. Regardless of the stressors affecting these systems it could be argued that since the effects of canopy disturbance resulted in a somewhat permanent or long-lasting shift in community composition, the combined effects of multiple stressors were antagonistic and resulted in a prolonged change in assemblage structure. It seems likely that the combination of stressors in these systems has passed a tipping point, with further large disturbance likely to create a permanent shift in community structure and production. Although unequivocal evidence of the combined effects of these stressors in real systems is difficult to ascertain, this research shows the difficulties in understanding multiple stressors in short term laboratory experiments. Furthermore, this study indicates that multiple stressors have the potential to alter the 'stable state' of intertidal communities and further disturbances of canopy fucoids could lead to wide-scale reductions in primary production. Future research would benefit from understanding how multiple stressors affect community structure and hence various forms of ecosystem function over longer temporal scales *in situ*.

Annual primary production

Modelling annual production of macroalgae over entire reefs

7.1. Introduction

Primary production is arguably the most important function of biological communities. In the marine environment the quantity and fate of primary production plays a vital role in regulating climate *via* the global carbon pump (Longhurst & Harrison 1989; Emerson et al. 1997). Despite the large amount of research on primary production of phytoplankton (Antoine et al. 1996; Karl et al. 2001; Behrenfeld et al. 2006), relatively few studies have attempted to quantify production on a large scale in macroalgal assemblages (Duarte & Ferreira 1997). Although rocky reef habitat reflects a small proportion of the oceans, these are known as some of the most productive systems on earth (Whittaker & Likens 1973; Mann 1973) and support some of the most diverse ecosystems in the temperate marine environment. Understanding the quantity of primary production in these systems will help our understanding of the nutrient cycling in nearshore systems.

Existing models of large scale production in macroalgae are generally based on measurements of physical growth, often using harvesting techniques (Duarte & Ferreira 1997). More recently, primary production of *Macrocystis pyrifera* was estimated by a sophisticated model of spatial and temporal variation in physical growth rates (Reed et al. 2008). One of the problems involved in estimating primary production from rates of physical growth, however, is the unknown quantity of biomass lost due to processes such as herbivory, abrasion, partial mortality and reproduction. To account for these losses, models integrating physiological primary production (through incubations measuring oxygen production or carbon fixation) with environmental variables, such as surface irradiance may prove vital (Ferreira & Ramos 1989). However, for these models to be accurate, several problems associated with extrapolating annual production from short term incubations must be accounted for. These include (1) understanding how much light energy is available throughout the year, (2) understanding how the photosynthetic response of algae varies as a function of irradiance in field conditions, preferably on a per area basis, (3) the effects of emersion on production (Ferreira & Ramos 1989) and (4) if or how production varies across tidal gradients. Furthermore, to predict primary production over large scales, accurate estimates of reef area and relative species cover must be available.

Determination of primary production using physiological methods may help uncover the quantity of primary production in macroalgal assemblages on annual scales, while taking only a fraction of the time necessary for *in situ* measurements of physical

growth. In order to do this, primary production would have to be measured at an appropriate scale *in situ*, and extrapolated over an annual basis using *in situ* irradiance data. This would enable an estimate of whole assemblage primary production per area of reef surface and would provide a template for modelling primary production over greater spatial and temporal scales. To improve the accuracy of these models, the inclusion of seasonal variation in production and the effects of production would be necessary. Furthermore, the use of satellite images or aerial photographs provides a mechanism to scale up per area production to local or regional scales. For example, the use of satellite imagery to estimate cover and density of *Macrocystis pyrifera* has been done on several reefs in southern California (Cavanaugh et al. 2010) and has the potential to make estimates of whole reef primary production relatively straightforward. Although satellite imagery has the potential to become an extremely valuable tool, however, field measurements are vital to the understanding of satellite data (Cavanaugh et al. 2010).

This study aims to estimate primary production of macroalgal assemblages using *in situ* photorespirometry measurements, and model annual carbon production using *in situ* irradiance and temperature data. This will provide an accurate estimate of macroalgal assemblage production over annual scales. Furthermore, variation in production potential with temperature may also provide an estimate of the potential effects of climate change on macroalgal primary production over longer time scales. Although the use of photorespirometry measurements can give a comparative estimate of production in macroalgal assemblages, modelling this with annual irradiance data will give insight into the variables affecting primary production over longer time scales. Also, a greater understanding of primary production on a local or regional scale will provide an idea of the relative contribution of benthic macroalgal assemblages to near-shore primary production inputs.

7.2. Methods

Using primary production data for various assemblage types examined in previous chapters (Chapters 4, 5 and 6), P-E curves were fitted. The equation of these curves was then used to model the primary production of that assemblage type over an annual period. The equation was solved for Y (production in g C m^{-2} h^{-1}) using irradiance from *in situ* data loggers. This provided a model for the quantity of carbon fixed by each assemblage, per year, which when coupled with estimates of reef cover, gave an annual estimate of

carbon fixed per reef. Physiological oxygen production measured in these assemblages was converted to carbon fixation using a photosynthetic quotient of 1.1, as used in other studies on temperate algae (Littler & Arnold 1982; Hanelt et al. 2003). This model was used for estimating primary production of Wairepo and Jimmy Armers Reefs, Kaikoura, a stretch of reef approximately 1 km long, as well as North Reef, Moeraki.

7.2.1. *In situ irradiance and temperature logging*

Irradiance was logged for Wairepo Reef, Kaikoura and North Reef, Moeraki at two sites across two shore-heights. Logging was done using HOBO (Onset©) irradiance and temperature loggers. Cross-calibration with data from a LiCor meter (LI-192 quantum sensor) was used to convert irradiance measured by HOBO loggers into PAR irradiance in µmol m^{-2} s^{-1}. Loggers set to record irradiance and temperature at 5 minute intervals began logging in February 2008 and finished in March 2010. Loggers were set on the reef using stainless steel cages with no lids, the loggers were orientated to face upwards, and held in place using zip ties. Cages were fixed to the reef using 4 rawl plugs which were drilled into the substratum using a masonry drill and bolted through the cage sides. Care was taken in the vertical placement of the loggers and loggers were secured in a manner so that nothing covered the irradiance sensor. Loggers were replaced at approximately 3-month intervals with new loggers and were checked at least monthly for fouling. Loggers were placed into two zones, the mid shore dominated by *Hormosira banksii* and the low shore dominated by *Cystophora torulosa*. Loggers were placed outside the canopy of these species and a third logger was placed on bare rock below the canopy of *H. banksii* to gain an estimate of subcanopy irradiance.

7.2.2. *Modelling annual primary production*

Annual primary production per square metre of reef was modelled using P-E curves determined using incubations. Incubations for all species were done between summer 07-08 and summer 09-10. These incubations were done *in situ* on Wairepo Reef, Kaikoura, and North Reef, Moeraki. This was done for assemblages dominated by *Porphyra spp*, *H. banksii*, and *C. torulosa* assemblages at Wairepo Reef, and *H. banksii*, *C. torulosa* and *Durvillaea antarctica* assemblages at North Reef, Moeraki. The annual primary

production model used several parameters, these included: emersion and immersion, temperature, seasonal differences in P-E curves and respiration rates.

The curves generated to fit the production-irradiance data during immersion were third order polynomial equations. The equation for the curves was as follows:

Equation 1: $$y = A + Bx + Cx^2 + Dx^3$$

Where y is the production measured as grams carbon fixed per metre square per hour (g C m^{-2} h^{-1}), x is irradiance µmol m^{-2} s^{-1}. The third order polynomial used the fitting parameters A, B, C and D to explain the fit of the curve to the data using Levenburg-Marquardt optimisation algorithm. The equation was solved for y using irradiance (x) from *in situ* data. Curves were fitted from production of 5 replicate plots. The curves generated for production-irradiance data during emersion were also fitted by polynomial equations. The equation for the curves was as follows:

Equation 2: $$y = A + Bx + Cx^{1.5} + Dx^2$$

Unlike the curve for assemblages during immersion, this equation fits a saturation curve as opposed to a inflection curve (Fig. 7.1). During emersion the structure of macroalgal assemblages changes from a three-dimensional assemblage, to a flat two-dimensional assemblage. During emersion, the canopy covered all understory algae, which have been shown to play an important role in the rise in production at high irradiance (Chapter 4). Since evidence suggests that production of macroalgae persists during emersion (Williams & Dethier 2005; Golléty et al. 2008), these assemblages continued to photosynthesize during emersion, but due to structural changes, the P-E curves switched from inflection to saturation.

The change from inflection curves to saturation curves was determined using tidal models (pers. comm. Philip Gillibrand, NIWA). The tidal model was fitted against the annual irradiance data and cross-checked with *in situ* temperature to ensure an accurate fit. To model the effects of emersion on production, the P-E curve used was defined by a function which fitted equation 1 during immersion (when tidal height > defined height) and equation 2 during emersion (when tidal height < defined height).

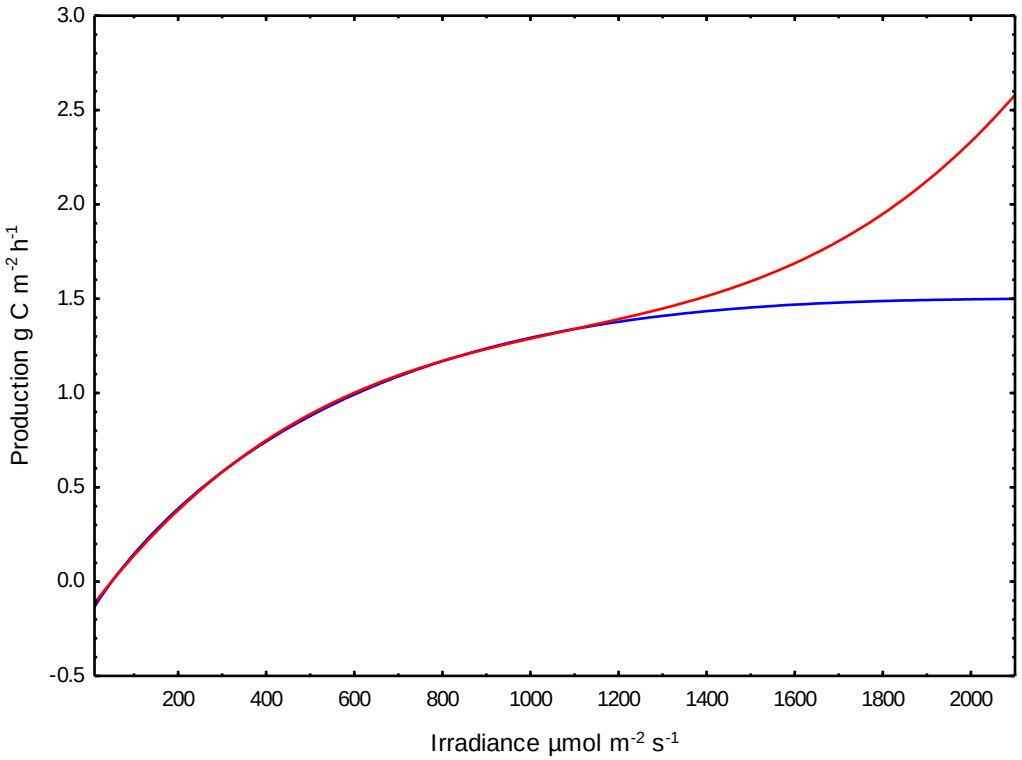

Figure 7.1. P-E curves fitted into annual production models. Red line shows the inflection curve (equation 1) fitted to the model during immersion and the blue line shows the saturation curve (equation 2) fitted to the model during emersion.

Although photosynthesis continued during emersion, evidence shows that once macroalgae have become desiccated, they cease to photosynthesize (Dring & Brown 1982). Given this, once temperatures exceeded a given value (modelled between 28-38˚C), net primary production was reduced to zero. Like tidal height, the effects of temperature on the reduction of photosynthesis was modelled as a function, where temperatures above a given threshold (between 28-38˚C) changed net production values to zero. The chosen temperature threshold range reflects the temperatures reached during emersion, with temperatures below 28˚C potentially including immersion.

Seasonal differences in P-E curves were fitted into the annual model by splitting annual irradiance data into four seasons and fitting the unique P-E curves defined for each season. Seasonal P-E curves were only derived for *H. banksii* as there was insufficient data for *C. torulosa* and *D. antarctica*-dominated assemblages. Since *Porphyra spp* was only present during spring, production was only modelled for the three months of spring. The production models for *C. torulosa*, *D. antarctica* and *Porphyra spp* included all other parameters, including tidal height, temperature, and respiration rate. The same

temperature range was used for all species, but the tidal range differed between species. The ranges of all parameters for all assemblages are shown in Table 7.1.

Table 7.1. Variable ranges used for the annual production model of each assemblage and the shore-height at which each assemblage occurs.

Species	Shore height	Tidal range (m)	Temperature range (˚C)	Respiration rate range (g C m^{-2} h^{-1})
Porphyra spp	High shore	0.85-1.05	28-38	-0.20 to -0.10
H. banksii	Mid shore	0.65-0.85	28-38	-0.20 to -0.05
C. torulosa	Low shore	0.45-0.65	28-38	-0.25 to -0.15
D. antarctica	Intertidal-subtidal fringe	0.25-0.45	28-38	-0.21 to -0.11

Once the model had been fitted to annual irradiance, temperature and tidal data, the P-E curves were fitted across the annual time-series, giving a value of carbon fixation during photosynthesis or carbon use during respiration (g C m^{-2} h^{-1}) for each 5 minute interval. The sum of all values was then combined to give an estimate of total carbon fixed per season for all assemblage types. Since primary production was estimated per hour, but a value of carbon fixation was generated every 5 minutes, the sum was divided by 12. Using the range of parameters (Table 7.1) multiple estimations of production were calculated for each season, giving an estimate of the standard error. The effects of each parameter alone on total production was also calculated.

To predict the production of these assemblages on a greater scale, the overall cover of *H. banksii* over Wairepo reef and North reef was estimated. This was done using aerial photographs, GIS referencing and area estimates using Google Earth Pro. Furthermore, seven years of annual sampling data were used to analyze the change in percent cover of *H. banksii* over time. This allowed a more realistic estimate of *H. banksii* cover relative to bare space.

7.2.3. *Temperature and production*

The effects of temperature on primary production potential was tested under laboratory and *in situ* conditions. Laboratory incubations were done using the same protocol as in Chapter 2, but the temperature of the water baths was manipulated to give four temperatures; 10, 15, 20 and 25˚C. Incubations were done at 4 levels of irradiance 0, 800, 1500 and 2000 µmol m^{-2} s^{-1} on *H. banksii* assemblages taken from Wairepo Reef,

Kaikoura. Assemblages of algae were removed along with the substratum using a hammer and chisel and taken to the laboratory (n = 8).

As well as lab-based incubations, natural variation in temperature *in situ* was used to test the effects of temperature on production in the field. As in laboratory tests, production was measured in assemblages dominated by *H. banksii* (n = 6). The temperature within incubation chambers was measured throughout incubations by internal loggers (HOBO, Onset©). Temperature was averaged over the duration of an incubation. However, incubations in the field are also confounded by variation in natural irradiance. To account for this, the effects of temperature on production were analysed within several ranges of irradiance. These were 1-200, 200-400, 400-800, 800-1200, 1200-1800 and 1800+ μmol m^{-2} s^{-1}. P-E curves were generated at temperature ranges of 8-13, 13-18 and 18-23˚C within each grouped level of irradiance. Furthermore, *in situ* respiration rates were determined within the same temperature ranges. These respiration incubations were done either during night, or else by covering the chamber with a dark cover to omit light.

To test the potential effects of elevated temperature on annual levels of primary production, the P-E curves generated at the three ranges of *in situ* temperature were used for scenario-based modelling. The curves were fitted to the models described above (temperature threshold set to 34˚C, at three tidal heights of 0.6, 0.7 and 0.8m). The three tidal heights provided the variation in the model (n = 3). Although temperature varies on a daily and seasonal basis, these data gave a proxy for the potential effects of increasing temperature on annual production.

7.3. Results

7.3.1. *In situ irradiance and temperature*

In situ irradiance and temperature data varied widely across the seasons (Table 7.2). As expected, summer had higher average and maximum irradiance, as well as higher average temperature, but interestingly autumn had the highest maximum temperature. There was little difference between maximum irradiance between autumn, spring and summer, but winter was significantly lower and reached only 1677.8 μmol m^{-2} s^{-1}.

Irradiance values in the low shore, mid shore, and mid shore subcanopy had much less variation than seasonal differences (Table 7.3). Maximum irradiances were relatively similar between temperature treatments, but average irradiance was higher in the mid shore than the low shore and much lower in the mid shore subcanopy. Average

temperatures followed much the same trend as average irradiance with mid shore showing the highest, then low shore, with subcanopy had the lowest average temperature.

Table 7.2. Irradiance and temperature during 4 seasons on Wairepo reef, Kaikoura. Data include seasonal average temperature and irradiance, maximum temp and irradiance, and minimum temperature. Data include emersion and immersion.

		Minimum	Maximum		Average	
Site	Season	Temp ˚C	Irradiance µmol m^{-2} s^{-1}	Temp ˚C	Irradiance µmol m^{-2} s^{-1}	Temp ˚C
Kaikoura						
	Autumn	1.9	1988.7	44.9	140.1 (2.2)	15.3 (0.05)
	Winter	-0.55	671.9	22.6	37.4 (1.2)	9.5 (0.01)
	Spring	0.34	2013.2	42.3	266.5 (2.1)	13.2 (0.2)
	Summer	6.3	2230.1	43.5	342.2 (3.5)	17.8 (0.01
Moeraki						
	Autumn	0.8	1910.2	17.07	130.1 (2.1)	12.8 (0.02)
	Winter	-2.1	491.3	17.9	30.3 (0.8)	8.4 (0.008)
	Spring	-0.3	2009.5	25.7	272.6 (2.6)	11.2 (0.014)
	Summer	6.1	2130.7	27.5	312 (3.3)	15.8 (0.02)

Table 7.3. Irradiance and temperature between August 2009 and November 2009 at different shore heights and beneath an *Hormosira banksii* canopy in the mid shore. Data include average temp and irradiance, maximum temp and irradiance, and minimum temperature. Data include emersion and immersion.

	Minimum	Maximum		Average	
Shore height	Temp˚C	Irradiance µmol m^{-2} s^{-1}	Temp˚C	Irradiance µmol m^{-2} s^{-1}	Temp˚C
Mid shore	1.8	2130.4	42.6	344.4	15.1
Low shore	2.5	2130.4	44.2	305	14.6
Mid shore Subcanopy	2.1	1951.1	35.1	155.7	14.3

Annual temperature and irradiance in the mid-tidal zone varied significantly over daily and seasonal scales (Fig. 7.2). Although the average annual temperature ranged between approximately 7-22˚C, daily changes could exceed 20˚C, showing the effects of emersion and immersion on reef temperature. In general, temperature and irradiance were very low over the winter months (May-August), but during spring and summer, irradiance levels were consistently high, with a large amount of recordings above 1500 µmol m^{-2} s^{-1}.

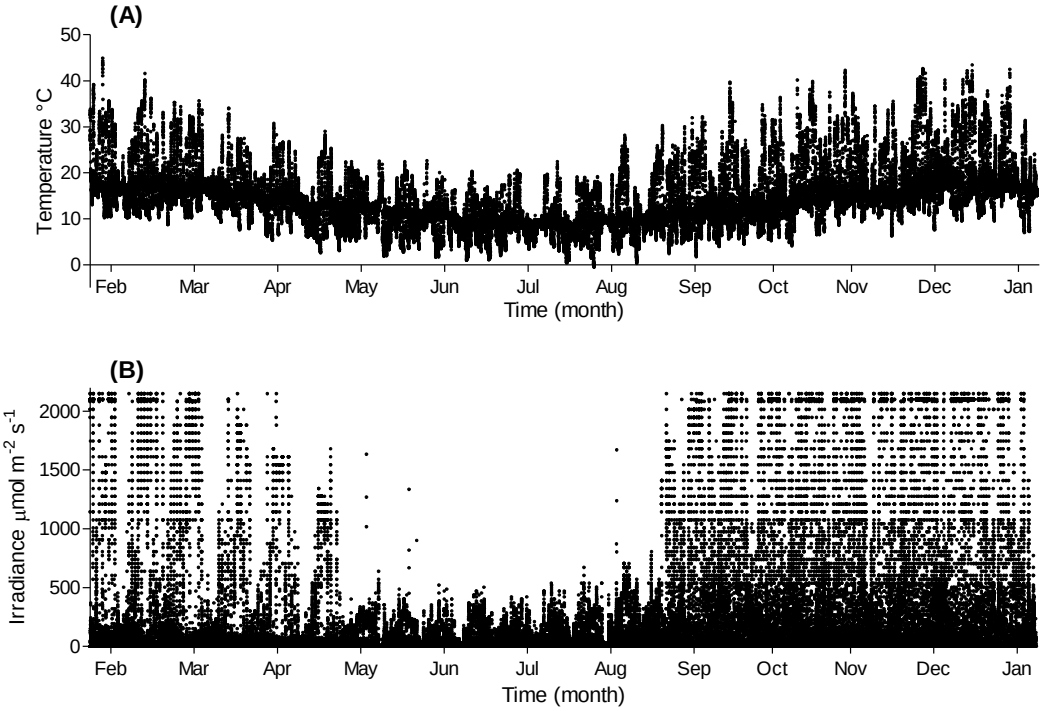

Figure 7.2. Annual temperature (A) and irradiance (B) in the mid-tide zone of Wairepo Reef, Kaikoura between January 2008 and January 2009.

7.3.2. *Annual primary production of macroalgal assemblages*

Annual predictions of primary production were determined using P-E curves of entire *Hormosira banksii* assemblages which were then fitted to annual irradiance using several parameters, including temperature and tidal height (Fig. 7.3). During emersion, the P-E curves shifted from the inflection curve to the saturation curve, as seen in the red shaded box (Fig. 7.5 A C and D). Also when temperatures exceeded a threshold value (in this case 32˚C), primary production of the assemblage stopped, as seen in the blue shaded box (Fig. 7.5 B and D).

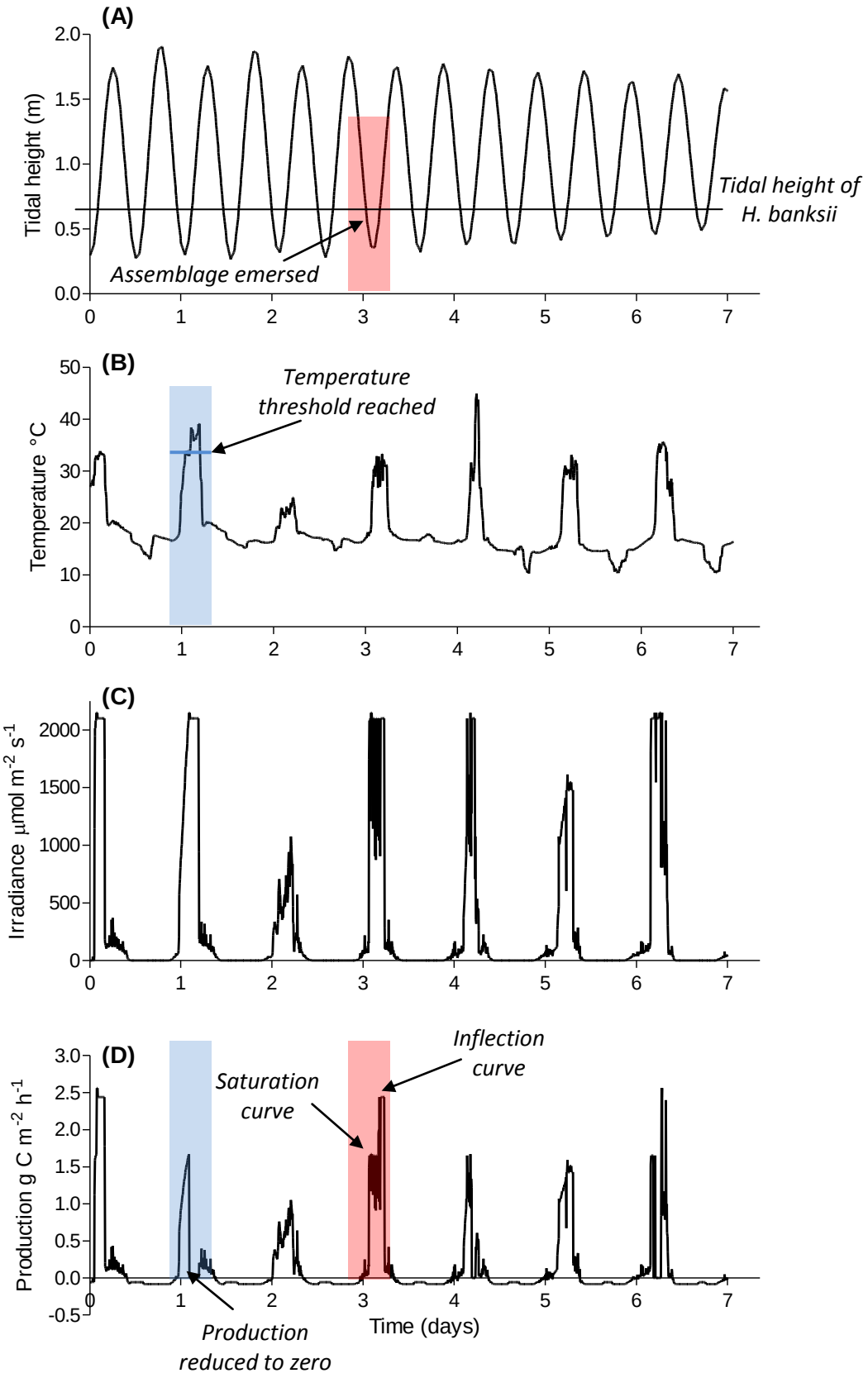

Figure 7.3. Predicting primary production of *H. banksii* using modelled tidal height (A), raw data from *in situ* temperature loggers (B) and raw data from *in situ* irradiance loggers (C). Calculated instantaneous primary production using these parameters shown in graph (D). Data from one week period during February 2008.

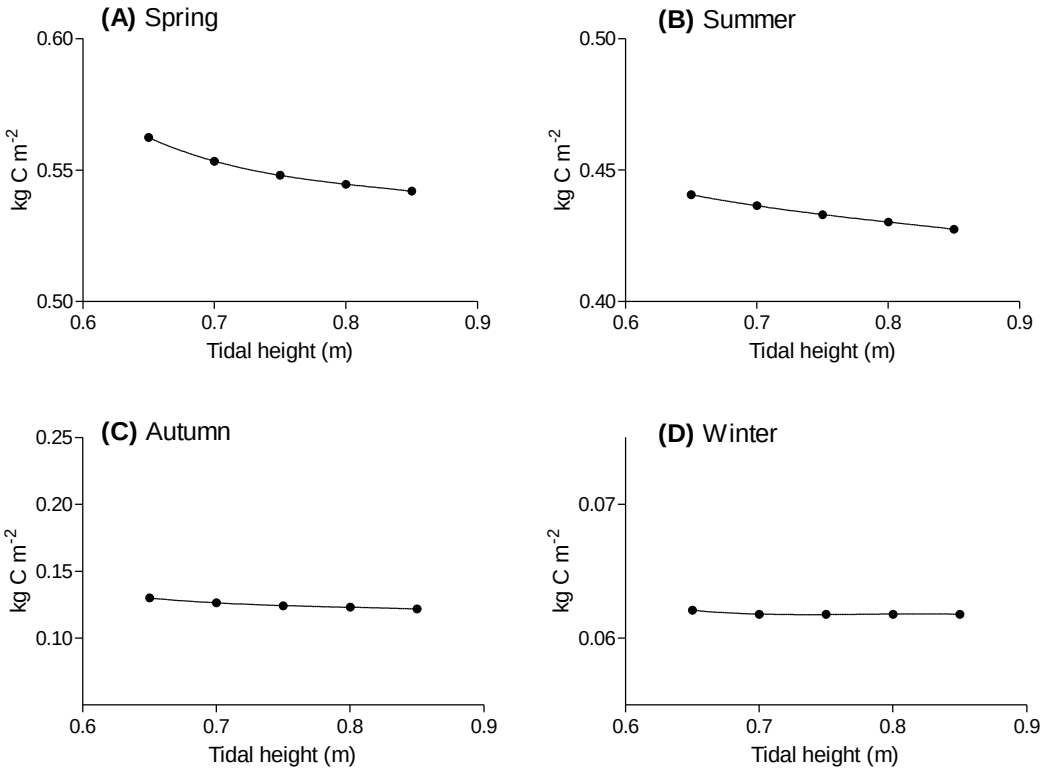

Figure 7.4. Effects of tidal height of emersion on total production per season (of equal length) of *H. banksii*-dominated assemblages during each season. Low tidal height results in shorter emersion time, whereas higher tidal heights result in longer emersion time.

The effects of shifting the tidal height at which *H. banksii* dominated assemblages became emersed had only a small impact on modelled primary production (Fig 7.4). Tidal height of emersion showed that as predicted tidal height of the community decreased, which increased the immersion time, primary production increased. This was more obvious during spring and summer, but had very little effect on production during winter and autumn. This is due to the lower irradiance during autumn and winter, with relatively few irradiance values above 1200 µmol m^{-2} s^{-1} where the inflection curve becomes important to total primary production.

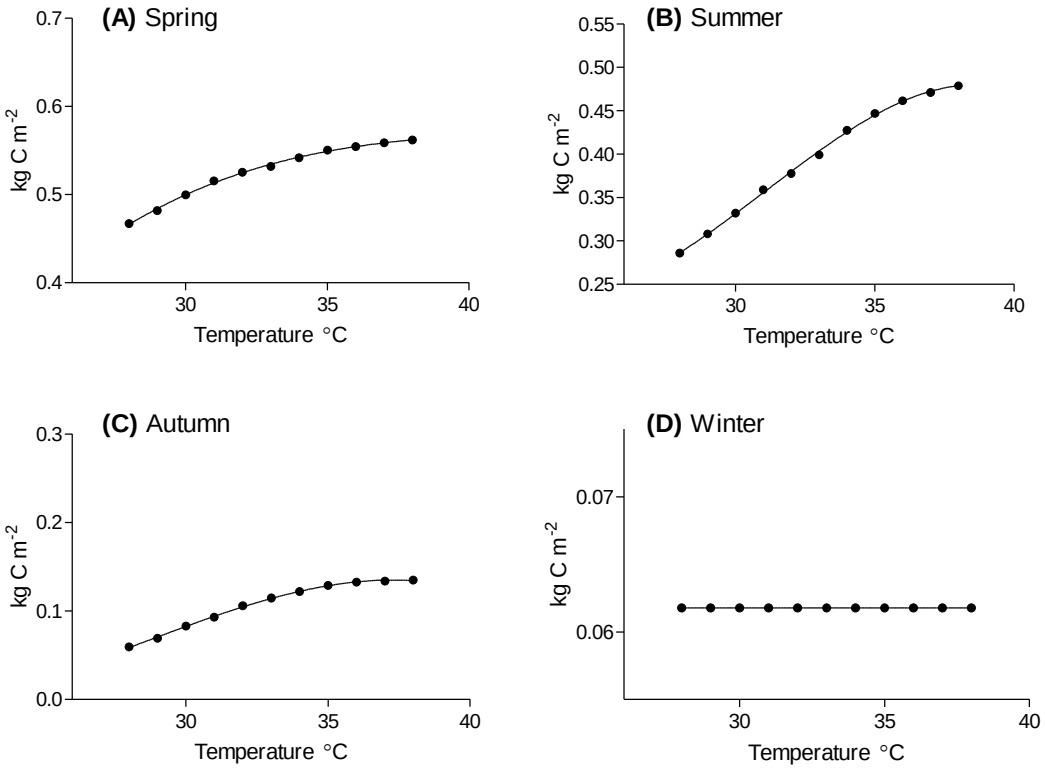

Figure 7.5. Effects of temperature threshold on production per season (of equal length) of *H. banksii*-dominated assemblages during each season. During periods when ambient temperatures exceed the threshold, net production is reduced to zero.

The threshold at which temperature inhibited photosynthesis had a greater effect on total modelled primary production than tidal height (Fig 7.5). At lower threshold temperatures, total primary production decreased due to increased frequency of temperature values above the threshold. The effects of shifting the threshold indicated that higher threshold values increased production, but above 35˚C, increasing the threshold further had little effect on production due to fewer temperature readings above that threshold. The effects of manipulating the temperature threshold were greatest in the summer, due to higher frequency of hot days. However, during winter, changing the threshold had no effect on production, which showed that temperature never exceeded the lowest threshold value of 28˚C.

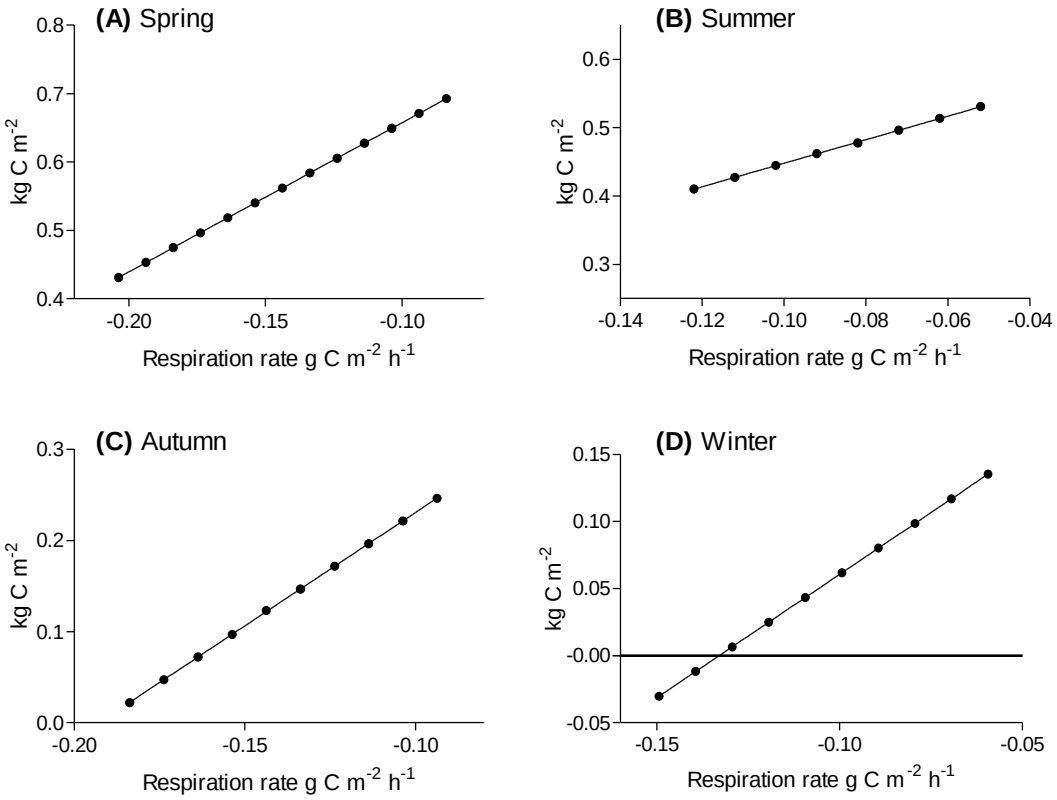

Figure 7.6. Effects of respiration rate g C m^{-2} h^{-1} on production per season (of equal length) in *H. banksii*-dominated assemblages.

Changing the respiration rate had a large effect on total modelled net primary production during all seasons (Fig. 7.6). As opposed to tidal height and temperature, respiration rate had a linear effect on net production during all seasons. Actual measured respiration rate varied throughout the seasons with -0.15 g C m^{-2} h^{-1} spring, -0.09 g C m^{-2} h^{-1} summer, -0.14 g C m^{-2} h^{-1} autumn, and -0.11 g C m^{-2} h^{-1} winter. Manipulating respiration rate had a minimal effect in summer, but had a large effect during all other seasons. During winter, increasing respiration rate affected net production, with respiration rates above -0.13 g C m^{-2} h^{-1} causing a net carbon loss. Overall, respiration rates had the largest effect (compared to temperature and shore-height) on modelled net primary production across all seasons.

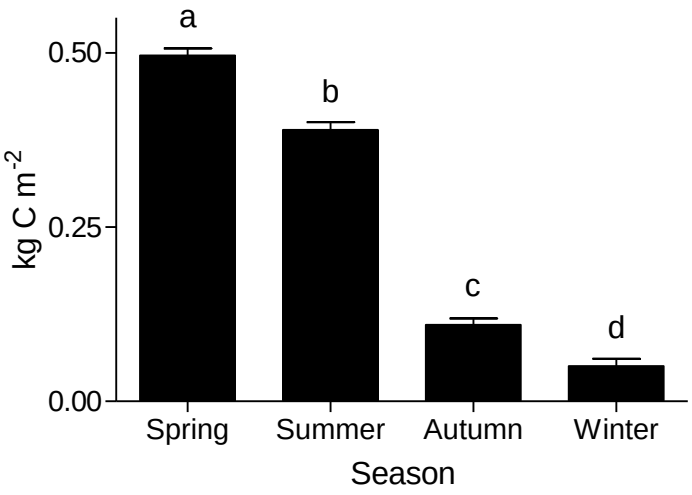

Figure 7.7. Seasonal primary production (±SE) of *H. banksii* assemblages. Seasonal replication derived from the range of input parameters (Fig. 7.6, 7.7 and 7.8). Significant difference shown by different letters.

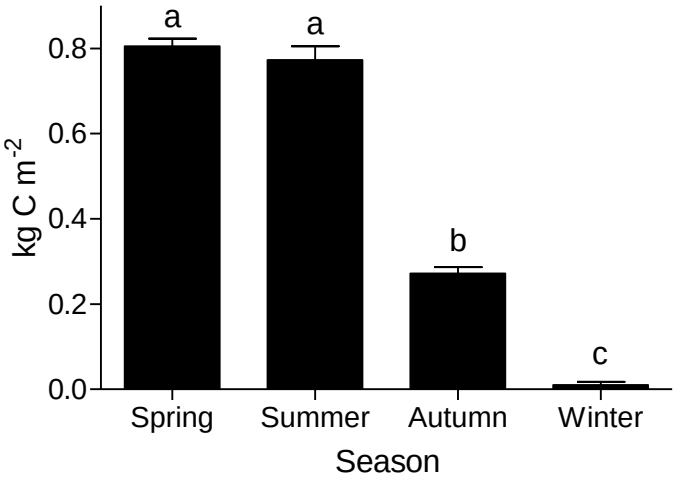

Figure 7.8. Seasonal production (±SE) of *Cystophora torulosa*-dominated assemblages. Seasonal replication derived from a range of input parameters, with tide ranging between 0.45 and 0.65m, temperature between 28-38˚C and respiration between -0.15 and -0.25 g C m^{-2} h^{-1}. Significant difference shown by different letters.

Average primary production showed that spring and summer were the most productive months, whereas autumn and winter represent only 17% of annual production (Fig. 7.7). One-way ANOVA showed a significant effect of season on production ($F_{3,90}$ = 411, p < 0.0001), with a significant difference between all Tukey's post-hoc test comparisons (q > 5.1, p < 0.01). Interestingly, despite having the highest average irradiance, summer was not the most productive month. The parameter which had the largest effect on production during summer was the threshold temperature, which may be

the cause for the higher production during spring (Fig. 7.7). The high frequency of warm days may result in much reduced production during summer.

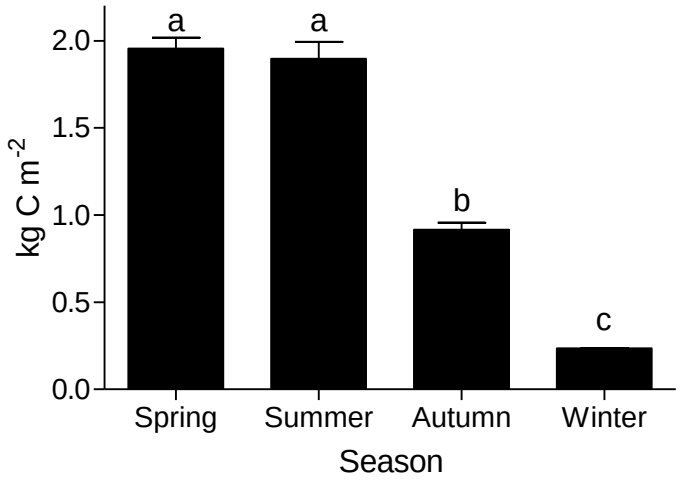

Figure 7.9. Seasonal production (±SE) of *Durvillaea antarctica*-dominated assemblages. Seasonal replication derived from a range of input parameters, with tide ranging between 0.25 and 0.45m, temperature between 28-38˚C and respiration between -0.11 and -0.21 g C m^{-2} h^{-1}. Significant difference shown by different letters.

Average production of *Cystophora torulosa* was the highest in spring and summer, with very low production during winter (Fig. 7.8). One-way ANOVA showed a significant effect of season on production ($F_{3,44}$ = 368, p < 0.0001). Tukey's post-hoc tests showed significant differences between all seasons (q > 12.9, p < 0.001) except summer and spring. Spring and summer production represents 85% of total annual production, whereas winter and autumn production is only 15% of annual production.

Like *C. torulosa*, average production of *Durvillaea antarctica* showed high production in spring and summer, with very low production during winter (Fig. 7.9). One-way ANOVA showed a significant effect of season on production ($F_{3,36}$ = 185, p < 0.0001). Tukey's post-hoc tests show a significant differences between all seasons (q > 11.2, p < 0.001) except summer and spring. Spring and summer production represents 75% of total annual production, whereas winter and autumn production is only 25% of annual production.

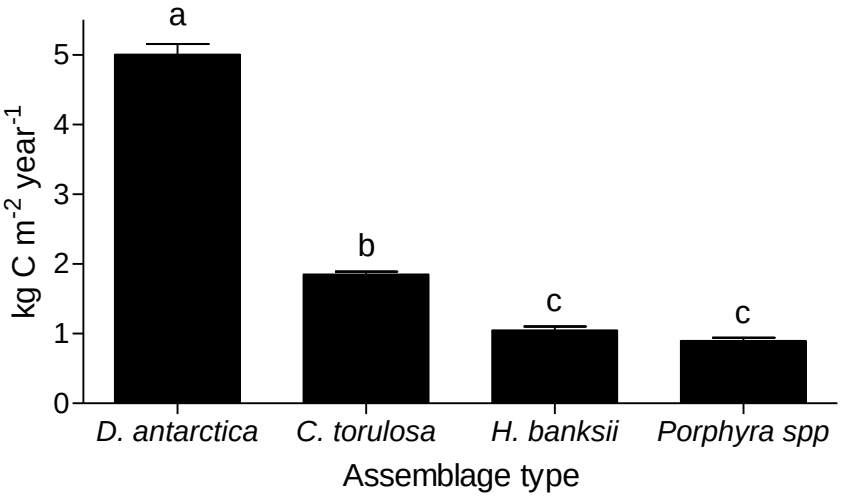

Figure 7.10. Total annual production (±SE) of four assemblage types *D. antarctica, C. torulosa, H. banksii* and *Porphyra* spp. Significant difference between assemblages shown by different letters.

Total annual production of four assemblage types shows increasing production down a shore-height gradient, with the low shore *D. antarctica* showing the highest annual carbon fixation (Fig. 7.10). One-way ANOVA showed a significant effect of assemblage type on production ($F_{3,21}$ = 538, p < 0.0001), with Tukey's post-hoc tests showing significant differences between all assemblage types (q > 10.5, p < 0.001), except *H. banksii* and *Porphyra spp*. *D. antarctica* had over double the production of the next most productive species, *C. torulosa*. Although *Porphyra spp* had the lowest annual production, this ephemeral species is only present during spring months, showing very high production over only three months.

7.3.4. *Modelling production across multiple habitats on whole reef scales*

The high shore sites at both Kaikoura and Moeraki had very stable cover of *H. banksii*, ranging between 80-100% cover over 6 years (Fig. 7.11). Wairepo reef averages approximately 90% *H. banksii* cover, whereas the North reef site averages 85% cover. In order to estimate total reef cover, the average cover of *H. banksii* allows us to estimate the relative proportions of reef covered by productive fucoid assemblages and less productive turfs or bare space. To estimate annual production on Wairepo reef, 80-90% of the total reef has the same production potential as the assemblages tested in

photorespirometry incubations. The other 10-15% of the reef for the purposes of the model is considered as non-photosynthetic bare space.

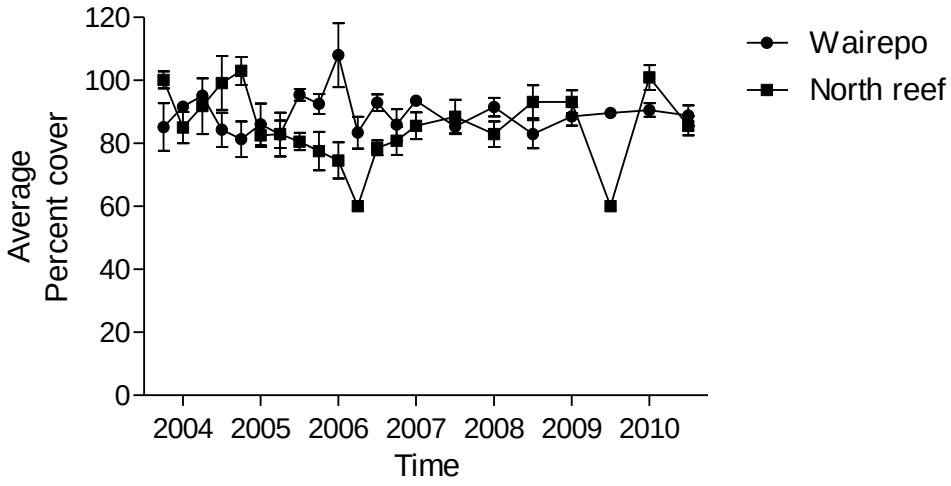

Figure 7.11. Average percent cover (±SE) of *H. banksii* at Wairepo reef Kaikoura and North reef Moeraki, in high-shore assemblages.

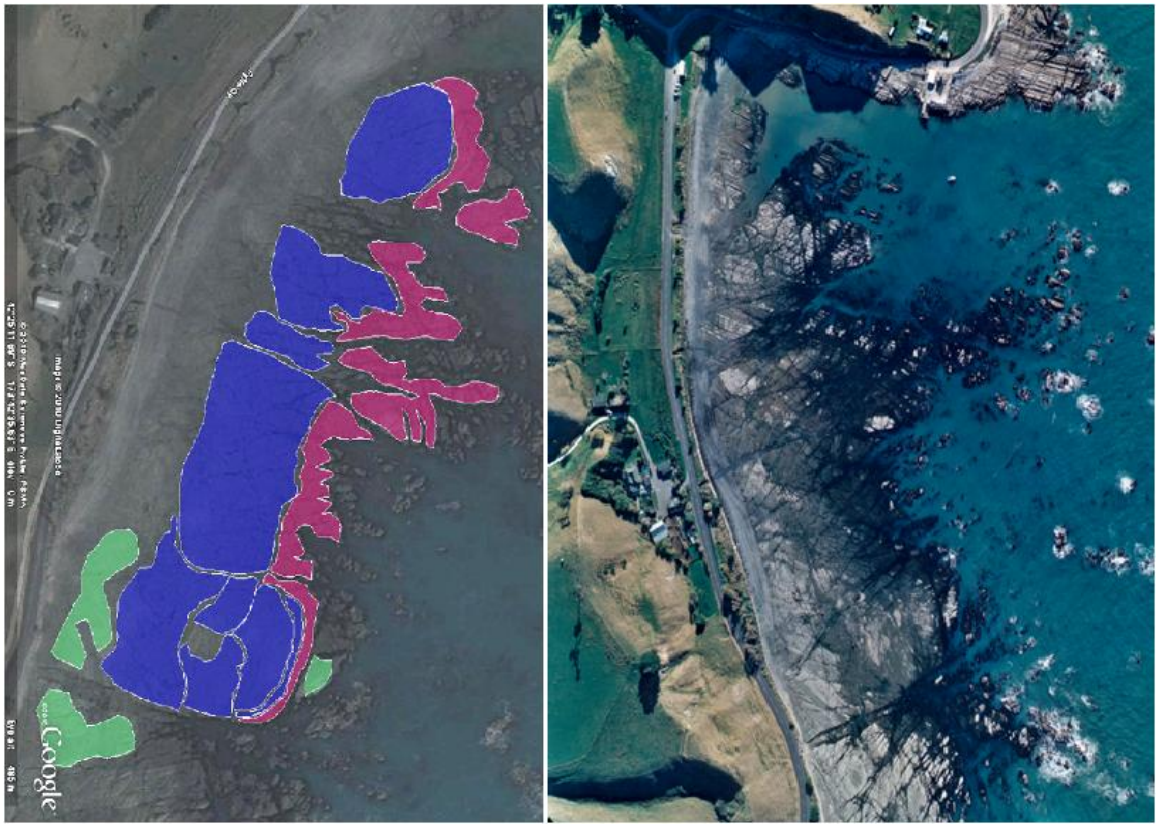

Figure. 7.12. Habitat mapping of Wairepo Reef, Kaikoura. Habitat area calculated using polygons in Google Earth, blue polygons represent *H. banksii*, pink represent *C. torulosa* and green represents *Porphyra spp*.

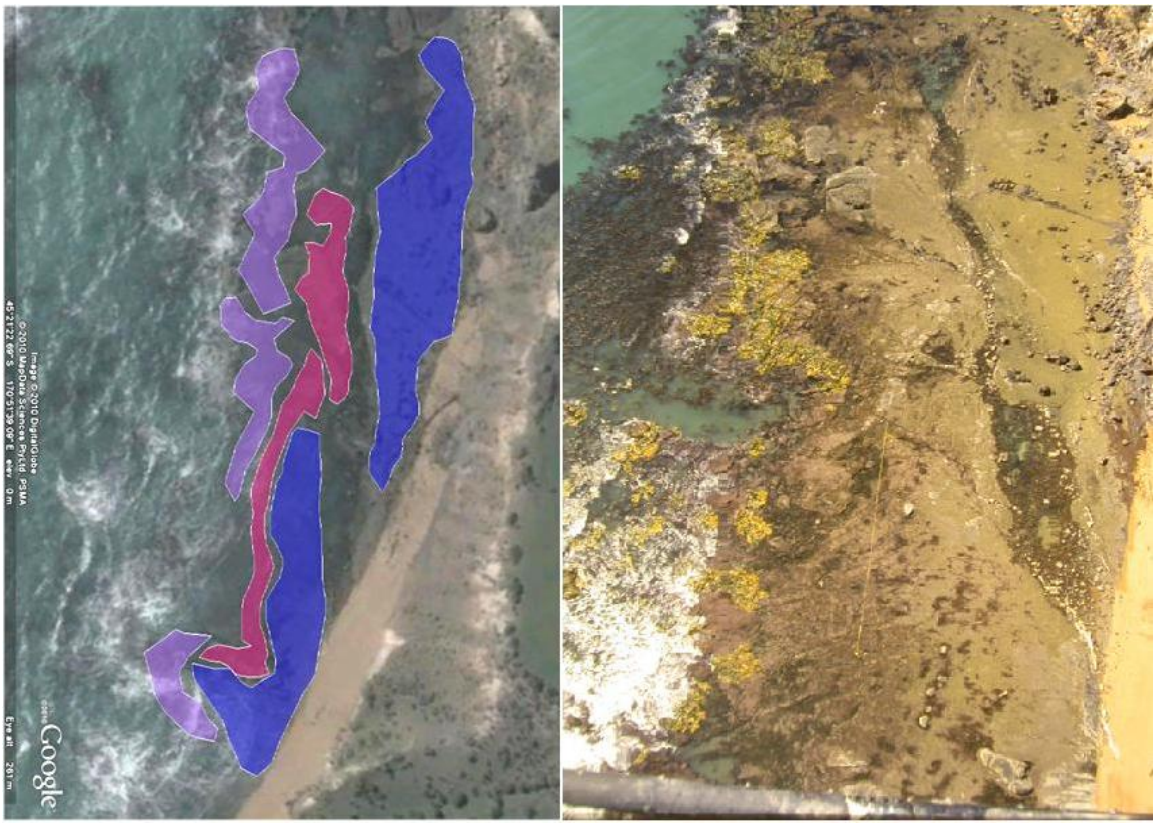

Figure. 7.13. Habitat mapping of North Reef, Moeraki. Habitat area calculated using polygons in Google Earth, blue polygons represent *H. banksii*, pink represent *C. torulosa* and purple represents *D. antarctica*.

The area covered by various macroalgal assemblages on Wairepo Reef, Kaikoura and North Reef, Moeraki was estimated by sectioning the reef into portions (Fig. 7.12 and Fig. 7.13). The size of Wairepo reef covered by algae equates to 61559 m^2, with areas of *H. banksii* equating to 41163 m^2, *C. torulosa* 15586 m^2 and *Porphyra spp* 4810 m^2 (Table 7.3). However, since approximately 10% of the *H. banksii* zone is bare space, the actual cover of *H. banksii* is 37593 m^2 giving a total macroalgal cover of 57989 m^2. The size of North reef, Moeraki covered by algae equates to 10479 m^2, with areas of *H. banksii* equating to 5873 m^2, *C. torulosa* 1915 m^2 and *D. antarctica* 2691 m^2 (Table 7.4). However, since approximately 15% of the *H. banksii* zone is bare space, the actual cover of *H. banksii* is 5286 m^2 giving a total macroalgal cover of 9892 m^2. When calculated as production per whole reef, biomass production was estimated at 72.5 tonnes of biomass per annum at Wairepo and 23.2 tonnes per annum at North Reef (Table 7.4).

Table 7.4. Habitat cover of various assemblages on Wairepo Reef, Kaikoura and North Reef, Moeraki and the corresponding primary production.

Habitat type	Kaikoura		Moeraki	
	Area covered m^2	Production tonne C $reef^{-2}yr^{-1}$	Area covered m^2	Production tonne C $reef^{-2}yr^{-1}$
H. banksii	37593	39.4	5286	5.5
C. torulosa	15586	28.8	1915	3.5
Porphyra spp	4810	4.3	-	-
D. antarctica	-	-	2691	13.5
Total	57989	72.5	9892	22.5

7.3.3. *Effects of temperature on production*

Gross primary production varied between 0.3-0.57mg C $gDW^{-1}h^{-1}$ over four levels of temperature and three levels of irradiance (Fig. 7.14). Two-way ANOVA showed a significant effect of irradiance ($F_{2,77}$ = 24.9, $p < 0.0001$), and temperature ($F_{3,77}$ = 13.1, $p < 0.001$), but no interaction effect. At lower irradiance (800 µmol m^{-2} s^{-1}) gross primary production was enhanced by increasing temperature. At the two higher irradiance levels (1500, 2000 µmol m^{-2} s^{-1}), production at 10˚C was lower than at the three higher temperatures.

Net production was greatly affected by temperature with high and low temperatures causing a reduction in primary production (Fig. 7.15). Two-way ANOVA showed a significant effect of irradiance ($F_{3,80}$ = 77.2, $p < 0.0001$) and temperature ($F_{3,80}$ = 4.1, $p < 0.001$), and an interaction (temperature x irradiance, $F_{9,80}$ = 2.4, $p < 0.05$). In all cases net primary production was reduced at 25˚C, indicating that temperature had exceeded the maximum range of *H.banksii*-dominated assemblages. Changes in production appear to be associated with a large rise in respiration rates at higher temperature as shown by the dark respiration results (0 irradiance). Although the decline in production at higher temperature may be due to higher respiration rates, the changing dynamics of production with increasing irradiance suggest that the combination of high irradiance and high temperature may have a negative effect on primary production.

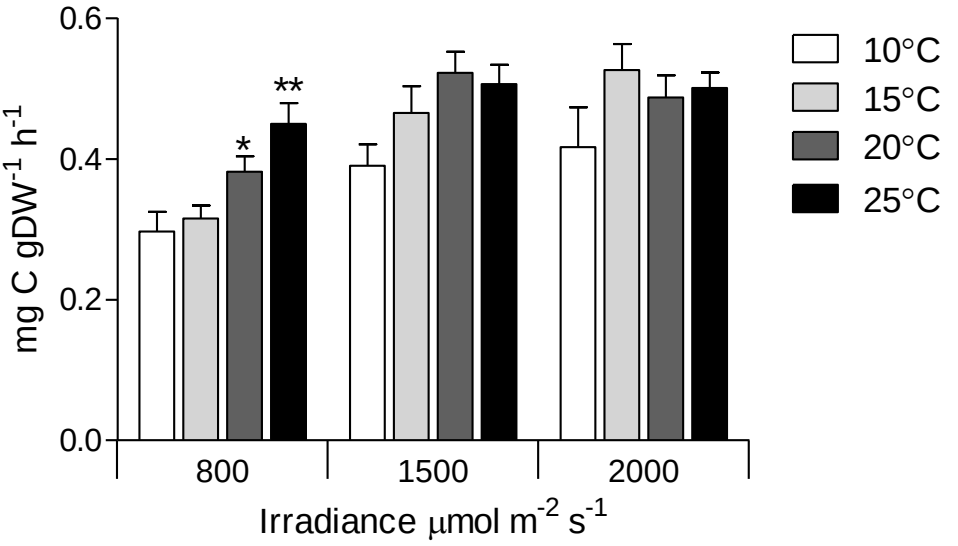

Figure 7.14. Effects of temperature on gross production (±SE) at three irradiance levels. Bonferroni post-hoc tests show a significant difference in production between 15 and 25˚C at 800 µmol m^{-2} s^{-1} (*t* = 3.2, p < 0.01), 10 and 20˚C at 1500 µmol m^{-2} s^{-1} (*t* = 2.8, p < 0.05) and between 10 and 25˚C at 800 µmol m^{-2} s^{-1} (*t* = 3.2, p < 0.01).

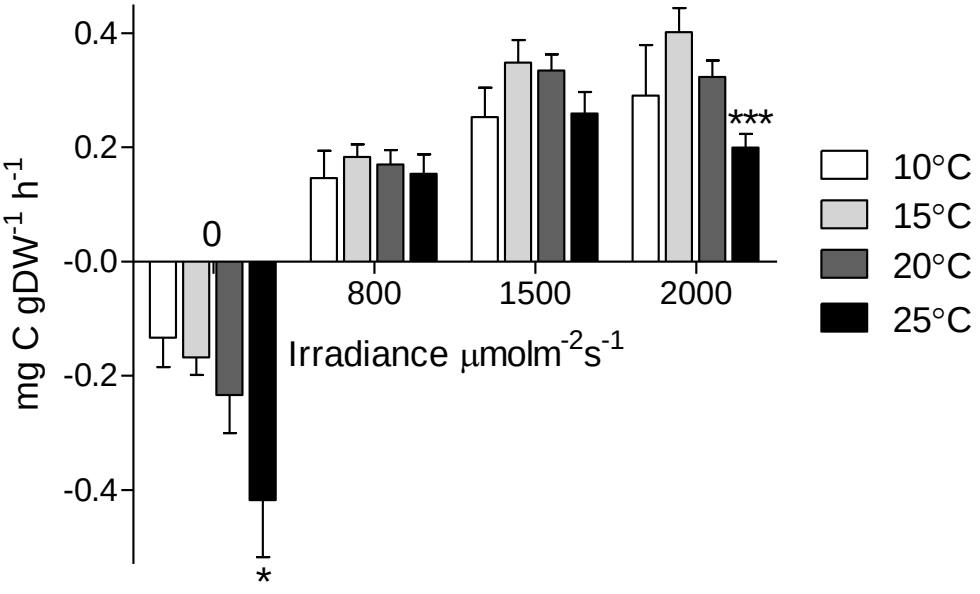

Figure 7.15. Net production (±SE) at 4 levels of irradiance under laboratory conditions at 4 temperature levels. Bonferroni post-hoc tests show a significant difference between 15 and 25˚C at 0 µmol m^{-2} s^{-1} (*t* = 3.0, p < 0.05), and 2000 µmol m^{-2} s^{-1} (*t* = 4.2, p < 0.001) and between 10 and 25˚C at 0 µmol m^{-2} s^{-1} (*t* = 3.4, p < 0.01).

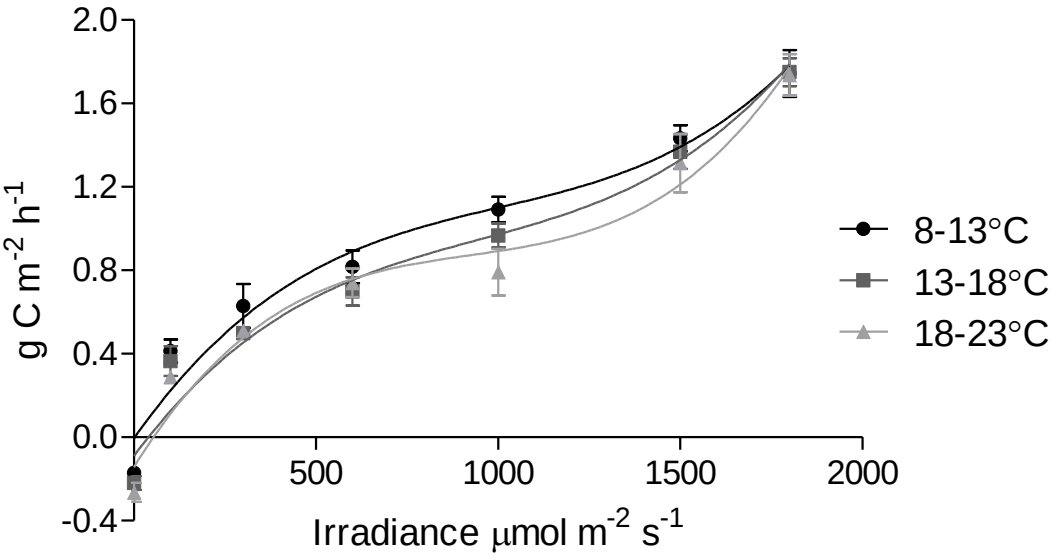

Figure 7.16. *In situ* P-E curves in mid-shore *H. banksii* assemblage at three ranges of temperature, 8-13, 13-18 and 18-23˚C.

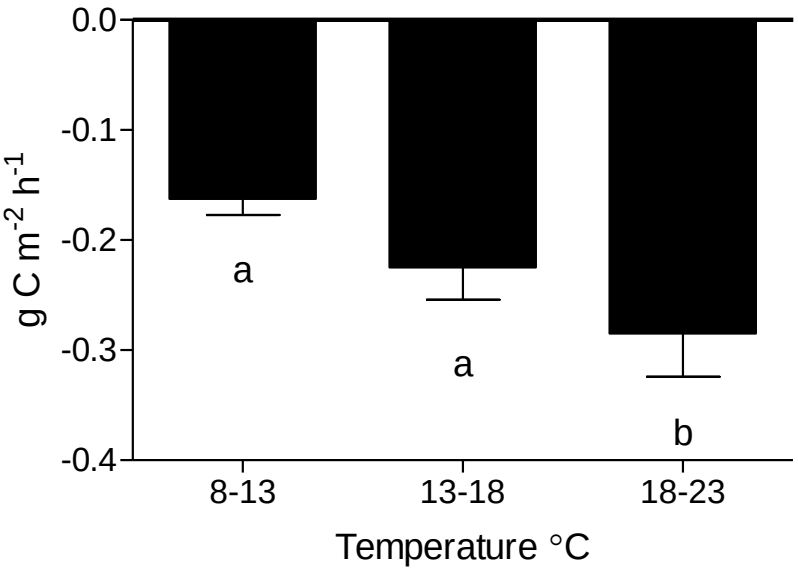

Figure 7.17. Comparison between *in situ* respiration rates (±SE) within the three temperature ranges 8-13˚C, 13-18˚C and 18-23˚C. Tukey's post-hoc tests show a significant difference between 8-13 and 18-23˚C ($q = 3.6$, $p < 0.05$).

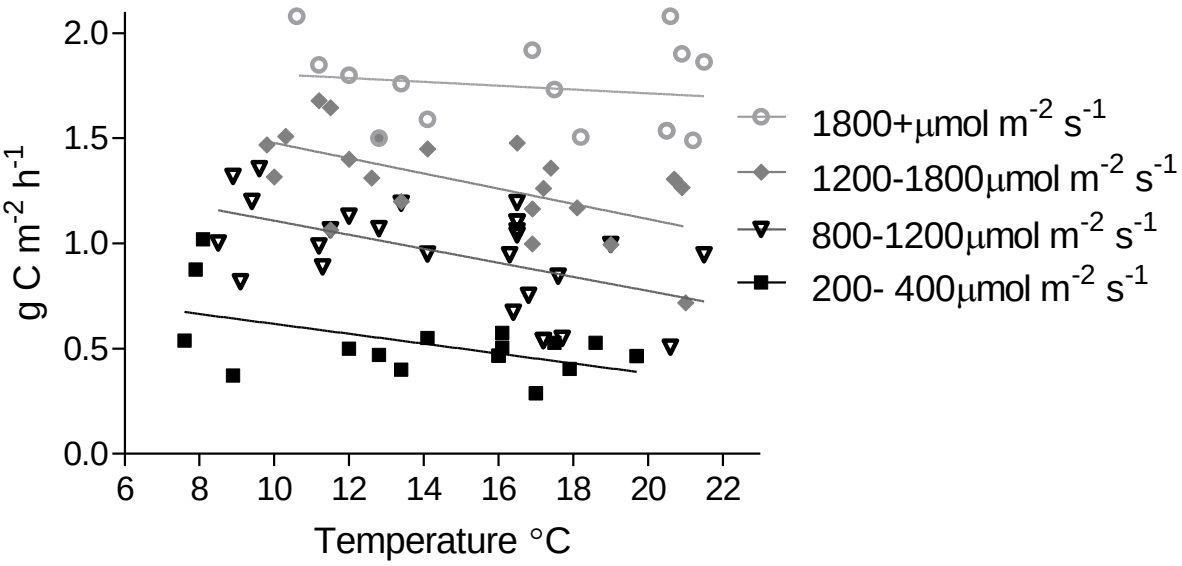

Figure 7.18. Production across temperature at 4 levels of irradiance: 1800+, 1200-1800, 800-1200 and 200-400 µmol m^{-2} s^{-1}.

The effects of temperature on production *in situ* were slightly different compared to laboratory results (Fig. 7.16). Although the curves indicate slightly lower production with increasing temperature, there was much less difference in production between temperatures at high irradiance. The major difference between *in situ* and lab methodology was the fact that both irradiance and temperature were controlled in the lab, whereas *in situ* data were grouped into ranges of temperature and irradiance. Variation in the *in situ* data may have caused some groups to be more heavily slanted towards the high/low end of irradiance or the high/low end of temperature. Like laboratory data, *in situ* respiration rates increased as temperature increased (Fig. 7.17). One-way ANOVA shows a significant effect of temperature on respiration rate ($F_{2,15} = 3.9$, $p < 0.05$).

When the effects of temperature on production were viewed across a temperature gradient, there was a strong relationship (Fig. 7.18). These data indicated a decrease in production with increasing temperature at 4 levels of irradiance. Linear regressions showed a significant negative effect of increasing temperature at 200-400 ($r^2 = 0.29$, $F_{1,17} = 6.9$, $p < 0.02$), 800-1200 ($r^2 = 0.27$, $F_{1,25} = 9.5$, $p < 0.01$), 1200-1800 ($r^2 = 0.35$, $F_{1,19} = 10.2$, $p < 0.01$), but not at 1800+ µmol m^{-2} s^{-1}. Although the effect of temperature on production may be harder to detect *in situ*, it appears that higher temperatures had a negative effect on production in macroalgal assemblages.

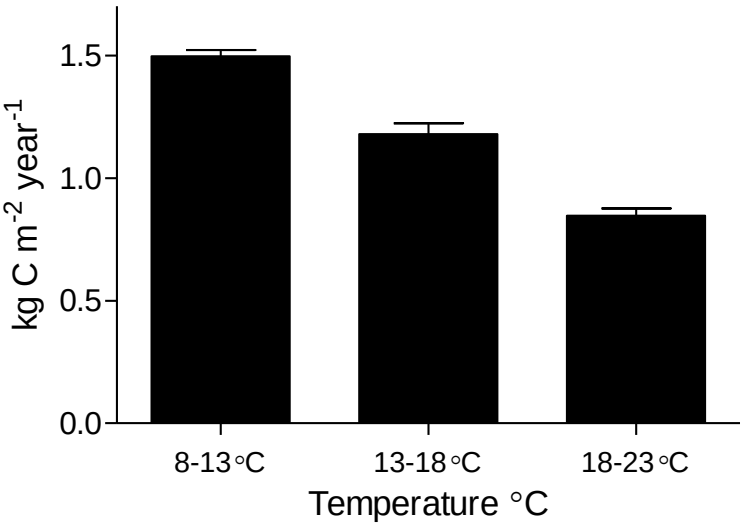

Figure 7.19. Effects of temperature on annual net production (±SE) of *H. banksii* assemblages. Annual production calculated by fitting curves from Fig. 7.6 to annual irradiance. Tukey's post-hoc test show a significant difference between 8-13 and 13-18˚C (q = 8.4, p < 0.001), 8-13 and 18-23˚C (q = 17.4, p < 0.001), as well as 13-18 and 18-23˚C (q = 9.1, p < 0.001).

Including the effects of temperature on annual production models showed there was a negative effect of increasing temperature on biomass production (Fig. 7.19). One-way ANOVA showed a significant effect of temperature ($F_{2,6}$ = 48.1, p < 0.01). Although this model fitted a P-E curve from a set temperature range across annual data, which has a large variation in temperature on daily and seasonal scales, it shows the potential effects of increased temperature on potential production. Despite the small variation in production caused by temperature in Fig. 7.16, when modelled across a year of irradiance, these small differences have a large effect. Much of the effects of increasing temperature appeared to be related to increased respiration rates at higher temperatures.

7.4. Discussion

7.4.1. *Annual primary production*

Models of annual carbon fixation show higher production at lower shore heights, as is seen from the maximum production of each assemblage type (Chapter 5). Therefore, it is not surprising that when modelled across a whole year these inherent differences in assemblage P-E curves give similar results. However, the seasonal red algae *Porphyra spp*, which are the most productive species throughout most of the irradiance range, show lower production than the other assemblages on an annual basis. Genera such as *Porphyra* are known as some of the most productive species on earth (Littler & Littler 1980; Littler & Arnold 1982), yet due to their ephemeral nature, are less productive than perennial species on an annual basis. *Porphyra spp* occur primarily in late winter- early spring with large blooms present for only 2-3 months. Even so, they are able to proliferate for very short periods and still reach annual production levels close to those of perennial species. Furthermore, the fast turnover of these species may result in fixed carbon being quickly available to the near-shore detrital food-web, as compared to being locked up in standing perennial biomass.

In the *Hormosira banksii* mid-shore assemblage, there was a significant amount of variation in primary production throughout the year. P-E curves generated for each season indicate slight differences in light use dynamics, particularly in winter when there is an increased efficiency of light use at lower intensities (Chapter 5). However, even with this increased efficiency, production during winter was less than a quarter of that in summer. The most likely explanation for this is the markedly lower average irradiance levels during winter and the greater time of low or zero light. During hours of darkness, not only is primary production not occurring, but respiration is continuing, thereby increasing the metabolic cost to the algae. This suggests that the quantity of light and respiration rates may be the most influential factors in predicting annual primary production. Furthermore, manipulation of the parameters shows that different factors have a greater influence on production in different seasons. The temperature at which photosynthesis stopped had the greatest effect during summer, whereas tidal height (and therefore immersion) had a greater effect during spring. Respiration rate had a similar effect during all seasons, but was less pronounced during summer. These effects allow primary production to be modelled while considering multiple factors, and have the potential to become a powerful tool in examining the drivers of large-scale primary production in intertidal systems.

Table 7.5. Estimations of annual primary production for a range of macroalgal and seagrass species from a number of studies.

Species	Primary production	Reference
Hormosira banksii	0.8- 1.3 kg m^{-2} yr^{-1}	This study
Cystophora torulosa	1.7- 1.9 kg m^{-2} yr^{-1}	This study
Porphyra spp.	0.7- 1.0 kg m^{-2} yr^{-1}	This study
Durvillaea antarctica	4.7- 5.4 kg m^{-2} yr^{-1}	This study
Macrocystis pyrifera	0.42- 2.38 kg m^{-2} yr^{-1}	Reed et al. 2008
Posidonia sinuosa	0.6- 0.9 kg m^{-2} yr^{-1}	Cambridge & Hocking 1997
Posidonia australis	0.9- 1.1 kg m^{-2} yr^{-1}	Cambridge & Hocking 1997
Gelidium sesquipedale	0.16- 0.18 kg m^{-2} yr^{-1}	Duarte & Ferreira 1997
Fucus vesiculosus	0.4 kg m^{-2} yr^{-1}	Ferreira & Ramos 1989
Ulva lactuca	0.2 kg m^{-2} yr^{-1}	Ferreira & Ramos 1989
Gracilaria verrucosa	0.07 kg m^{-2} yr^{-1}	Ferreira & Ramos 1989

Estimates of annual primary production from this study are comparable to those of various other macroalgal and seagrass species (Table 7.5). The comparison of *H. banksii* and *Cystophora torulos*a with *Macrocystis pyrifera* indicates surprisingly similar levels of annual production (Reed et al. 2008). Production of *H. banksii* (on a per-area basis) is within the lower range of that of the very productive *M. pyrifera*, whereas production of *C. torulosa* falls within the upper range of *M. pyrifera*. Comparison of the relatively low biomass assemblage of *C. torulosa* with the large kelp forests of *M. pyrifera* would suggest that the estimates of *C. torulosa* production are overestimated. However, *C. torulosa* occurs in dense beds, whereas distances between *M. pyrifera* plants may be several meters, making the per area production of *M. pyrifera* lower. The production of *C. torulosa* in this study also includes the production of the associated algal assemblage. Furthermore, estimations of production of *M. pyrifera* may be very conservative, as production was measured by rates of tissue growth (Reed et al. 2008), resulting in a large amount of unaccounted for biomass loss through processes such as sloughing. The potential for production in *M. pyrifera* indicates that it is much more productive on a per-biomass basis than the fucoids tested in my study (Fig. 7.20). The erosion of tissue and loss of carbon through dissolved exudates may result in a large amount of unaccounted for biomass in studies measuring physical growth rates. Also, numerous other kelps and a

vast number of understory species inhabit giant kelp beds, which would make primary production much higher on a per-area basis than for giant kelp alone. Interestingly, the species with by far the highest production is *Durvillaea antarctica* from this study. Per metre square, this species is more productive than the large *Macrocystis* forests. Although the production estimate for *M. pyrifera* may be conservative, this evidence suggests that these low intertidal/immediate subtidal beds of *D. antarctica* may be some of the most productive assemblages on earth. This is not completely surprising given that *D. antarctica* can exceed 10 metres in length, weigh up to 50 kilograms and can occur in densities of up to 5 adult plants per m^2. Furthermore, due to the size of the incubation chambers, only small *D. antarctica* plants could be analysed and there is likely to be a scaling effect of increasing thalli thickness on primary production in this species, potentially overestimating production of *D. antarctica*.

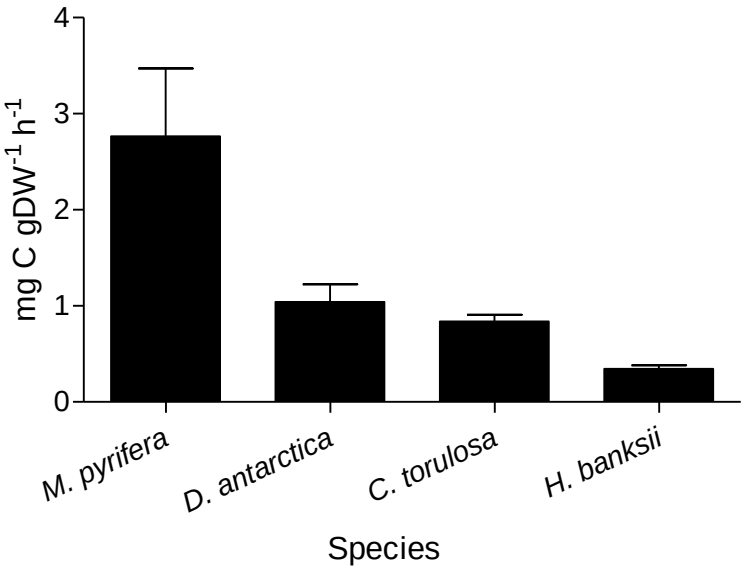

Figure 7.20. Comparative maximum production (±SE) of *M. pyrifera* (data from Arnold & Manley 1985), *D. antarctica*, *C. torulosa* and *H. banksii* (this study). Data show production determined using single thalli incubations.

The production of *H. banksii* is similar compared to fucoid species such as *Fucus vesiculosus* (Ferreira & Ramos 1989). Although potential production is likely to be higher in the *Fucus* genus (Chapter 5), the production of *H. banksii* in this study also considers the associated algal assemblage. Estimations of annual primary production in *H. banksii* assemblages is probably the closest to seagrass beds (Cambridge & Hocking 1997). Although these studies on seagrass and macroalgae use a range of methods to describe annual production, from measurements of physical growth or biomass change

(Cambridge & Hocking 1997; Reed et al. 2008), to models combining physiological growth with environmental variables (Ferreira & Ramos 1989; Duarte & Ferriera 1997), the results are relatively similar. This indicates that the model used in this study may predict primary production of entire macroalgal assemblages to a reasonable degree of accuracy. Although determining which models are accurate is a difficult task, this is one of the first attempts to define production of macroalgal assemblages as opposed to single species. Furthermore, my model takes into account all of the necessary factors for an accurate model as proposed by Ferreira & Ramos (1989). It uses an *in situ* measure of irradiance, compared to complex models of irradiance based on attenuation of light through water; it takes into account seasonal variation in algal production, and considers the effects of emersion, temperature and respiration. Furthermore, this research has the advantage of measuring production in whole assemblages *in situ*, making estimations of primary production more relevant to real ecosystems. Therefore, it provides a novel view on the potential primary production of intact macroalgal assemblages and using modern satellite images allows ecosystem scale estimates of primary production.

7.4.2. *Factors affecting annual primary production*

Temperature appears to have variable effects on the production of macroalgal assemblages, depending upon the irradiance environment. Although increasing temperature may have a positive influence on gross primary production at some irradiance levels, it significantly increases respiration rates. Therefore, the effects of increasing temperature on net primary production are negative at 20˚C and above. Results are similar under laboratory and *in situ* conditions at lower irradiance levels, but at high irradiance, increasing temperature did not have a strong negative effect on production *in situ*. However, *in situ* results may be less valid because variation in temperature is generally caused by seasonal variation. Seasonal variability in photo-acclimation may cause dramatic differences in photosynthetic efficiency at different irradiance levels. Although *in situ* data may show a trend of falling production with temperature, this may also be associated with variations in pigment content (Aguilera et al. 2002), i.e., higher pigment content during winter (cold temperatures) may result in higher production, as opposed to a direct effect of temperature. Therefore, the P-E curves for the different temperature ranges may contain variation from seasonal differences compared to physiological effects of temperature.

Despite the potential problems with the *in situ* data, laboratory data suggest a fundamental effect of temperature on net primary production in macroalgal assemblages. Although this study indicated a negative effect of temperature on net primary production (Fig. 7.15), other studies have shown a positive effect of temperature on net primary production at saturating irradiance (Davison 1991). This positive relationship is related to the increased speed of enzymatic processes, known as the Q_{10} effect, which increases production up until an optimum temperature, after which photosynthesis declines rapidly (Davison 1991). Also, some studies have shown that elevated temperatures can have a neutral effect on production (Henley et al. 1992). Such a relationship is most likely associated with a concurrent increase in photosynthesis and respiration, resulting in net primary production remaining unchanged. Although this study shows increasing gross primary production with temperature at lower irradiance, high temperature negatively affected net production particularly at high irradiance, possibly due to temperatures exceeding the optimum scope of the species in question. When net primary production is considered, it appears that the optimum operating temperatures of these assemblages are approximately 15-20˚C, determined by laboratory incubations. Although field based incubations suggest an optimum temperature between 8-13˚C, the data is complicated by photo-acclimation of the assemblages incubated during colder months. Furthermore, the combined effects of high temperature and high irradiance have been shown to negatively impact primary production, causing major photoinhibition (Henley et al. 1992; Bruhn & Gerard 1996). Such combined effects of high temperature and irradiance are routinely observed in bleaching events of coral and their zooxanthellae symbionts (Yellowlees & Warner 2003). The drop in production due to high temperatures in algal assemblages may be equivalent to the photoinhibition seen in coral species. Bruhn and Gerard (1996) showed that at temperatures exceeding 25˚C, high irradiance significantly increased photoinhibition in *Laminaria saccharina*. In this study, temperatures of 20˚C were high enough to elicit a negative effect. Differences in the temperatures at which strong negative effects are observed may be due to variation in the ability of the macroalgal species to cope with high temperature and irradiance, or assemblages of macroalgae may behave very differently to single specimens.

It is possible that the mechanisms operating at the assemblage level may be very different from those operating at the species level. For example, temperature can have very different effects on production at saturating vs. non-saturating irradiance levels (Davison 1991). At non-saturating irradiance, increasing temperature can have a negative

effect on primary production. The impacts of low light and high temperature has been observed in macroalgae (Davison 1991) and in seagrass (Lee et al 2007), showing that autotrophs growing in low light conditions have lower optimum temperatures for photosynthesis. This has interesting implications, given that in an assemblage species can be exposed to high light in the canopy and low light in the subcanopy. It is possible that although the canopy may be experiencing enhanced production due to Q_{10} effects of temperature on enzymatic processes, the subcanopy may be experiencing negative effects of temperature (Fig. 7.21). Evidence suggests that in benthic diatom communities, elevated temperature stimulates heterotrophic activity more than gross photosynthesis (Hancke & Glud 2004), indicating that the effects of rising temperature may have very different effects on whole communities, compared to species in isolation. In macroalgal assemblages, higher respiration in the canopy may be compensated for by enhanced production, but it is likely that high respiration rates in the subcanopy may be having an overall negative effect on assemblage primary production.

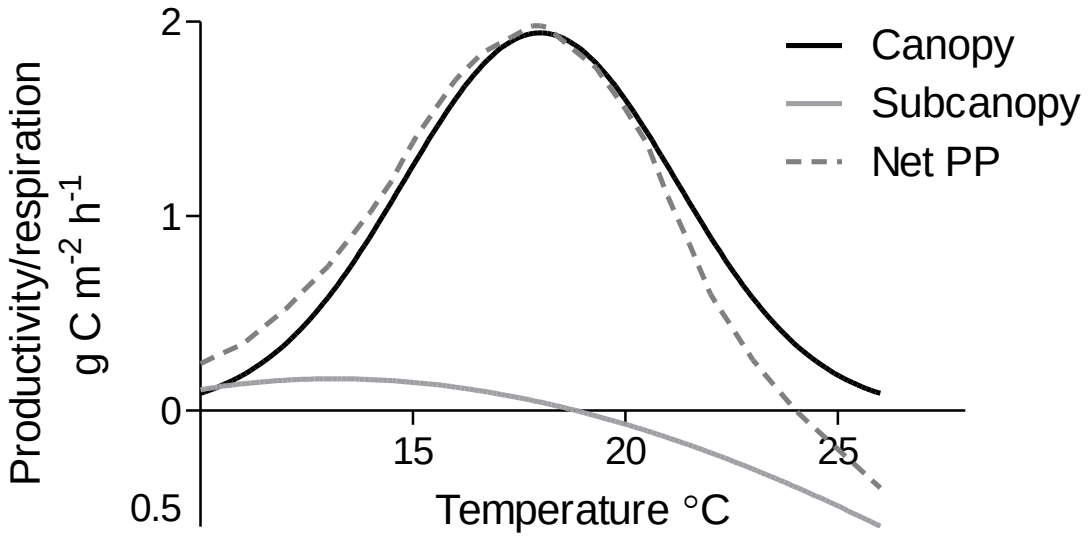

Figure 7.21. Hypothesised effects of temperature on production/respiration rates in the canopy and subcanopy species of a macroalgal assemblage.

Although respiration may have large effects on short term net production, higher respiration rates could have much larger effects over longer time scales. Although there was relatively little difference in the shape of the P-E curves at three *in situ* temperature ranges, when modelled with annual irradiance, there was a much more dramatic effect of temperature on production. The Q_{10} effect may help limit the impact of increased

respiration rate by enhancing production, but during the night, when no photosynthesis is occurring, a higher respiration rate could be extremely detrimental to net production over longer time scales. Furthermore, when respiration was manipulated in models of net primary production, it was probably the parameter with the greatest effect on net primary production during all seasons. These data suggest that although small temperature rises may have a negligible effect on primary production, the real effects may come in the increasing of respiration rates at night, leading to a large increase in the metabolic costs to these autotrophs.

Increasing oceanic temperature due to global warming may have potentially devastating consequences on the quantity of carbon fixed by marine macroalgae (Behrenfeld et al. 2006). Climate fluctuations can cause large scale shifts in the production of phytoplankton through alteration of surface nutrient dynamics (Stenseth et al. 2002). This research suggests that temperature may have a more direct effect on the production of macroalgal assemblages. Excluding any effects of temperature on nutrient dynamics, higher temperatures may be affecting macroalgal assemblages in two ways: 1) higher respiration rates, particularly during darkness may change the ratio of photosynthesis to respiration, decreasing long term net photosynthesis, and 2) the combination of high temperature and high irradiance may be increasing photoinhibition, thereby decreasing net production during periods of high irradiance as observed in coral reef zooxanthallae (Yellowlees & Warner 2003). El Niño and Pacific decadal oscillations are associated with changes in phytoplankton production which can result in large scale 'regime shifts' (Chavez et al. 2003). Changing primary production dynamics can have large flow-on effects on ecosystem functioning and have the potential to significantly alter population dynamics. Increases in oceanic temperature have the potential to directly influence net primary production by marine macroalgae. Furthermore, shallow coastal waters may be more heavily affected by climatic change than deeper oceanic systems. The effects of temperature on net primary production by macroalgal assemblages may help us understand the potential flow on effects to the wider ecosystem. Greater predictive power of the potential impacts of climate change may provide mitigation strategies for coastal fisheries, that are directly or indirectly reliant upon macroalgal primary production.

Macroalgal assemblages may give insight into the effects of rising temperature on production of autotrophic assemblages in general. The ability to test the impacts of rising temperature on an entire assemblage, comprised of several canopy layers exposed to

different irradiance environments is difficult when integrating biomass change over longer periods. In terrestrial systems, the need to integrate production over longer time-scales makes determination of production at a given irradiance difficult. This research has uncovered a unique fall in production with increasing temperature and irradiance which is not necessarily observed in a single species or specimens. Increasing temperature in a low irradiance environment has been shown to negatively affect primary production (Davison 1991), which has implications for the shaded subcanopy of autotrophic assemblages. The hypothesised relationship between net primary production and temperature (Fig. 7.21) predicts that, due to increased respiration in the subcanopy, overall assemblage production declines more rapidly than would be expected from the canopy alone at high temperatures. Respiration is a major determinant of the carbon balance of forests (Shaver et al 2000; Valentini et al. 2000). Such findings could be relevant for other photo-autotrophic systems where a shaded subcanopy is present, and could have significant implications for estimates of community respiration rates and, therefore, the impacts of climate change on carbon sequestration. Estimates of respiration based on theoretical or empirical knowledge of organism physiology have been used to estimate carbon balance in the oceans (López-Urrutia et al. 2006), but a lack of understanding of assemblage or community physiology may limit such results. Studies testing the effects of temperature on the relative Q_{10} of terrestrial plants indicate that in order to accurately model the effects of temperature, a temperature-corrected Q_{10} is required (Tjoelker et al. 2001). However, results from this study show that another level correction for whole assemblages is necessary to predict respiration rates. Understanding the relative roles of temperature, non-saturating irradiance and whole assemblage respiration/production may provide essential information on the potential impacts of climate change on carbon sequestration in autotrophic assemblages.

General discussion

Primary production in macroalgal assemblages: comparisons and contrasts with other ecosystems

8.1. General discussion

This thesis examined the primary production of macroalgae and their associated assemblages. I found key differences in the way assemblages, compared to single species, use light and report a unique P-E curve for *in situ* algal assemblages that occurred in numerous assemblages dominated by different species from different continents. Furthermore, non-random species loss, particularly the loss of canopy-forming species, had a significant effect on primary production of *in situ* assemblages, supporting the need for more biodiversity-ecosystem function studies to consider natural species composition and realistic species loss (Bracken et al. 2008). The aim of this thesis was to better understand the primary production of macroalgal assemblages and the factors affecting and driving production. Most evidence points to light being the key to the production of these assemblages, which showed no evidence of saturation of photosynthesis at high light levels. Furthermore, the three dimensional structure of macroalgal assemblages is critical to overall production, with the loss of canopy species significantly decreasing production. *In situ* measurements of assemblage production allowed me to calculate annual primary production on a whole reef scale by incorporating measurements of incident irradiance. This provided a relatively simple framework to estimate primary production over whole reefs, without intensive sampling of *in situ* growth rates. When primary production was modelled annually, several factors, which had a relatively small effect on net primary production in the short term, had a large effect on net primary production in the long term. In particular, respiration rate played an important role in models of annual carbon fixation. Furthermore, this research shows the importance of maintaining biodiversity and the vital role of key canopy-forming fucoids in enhancing resource complementarity of assemblages. This study, therefore, gives insight into the greatest potential threats to macroalgal assemblages, showing both short-term and long-term consequences of changes in environmental and biological variables.

8.2 Thalli to assemblages

The influence of canopy structure on primary production has been suggested by many authors, but little has been done in the marine environment to test the potential roles of various canopy layers on production. Experiments on aquatic plants are often performed on spatial scales much smaller than in natural systems (Beyschlag & Ryel 1998).

Therefore, production of a single thallus does not necessarily apply to whole plants or their associated communities. Similar to research by Binzer & Middleboe (2005), my study shows that experiments on the thallus scale should be avoided or treated with caution when predicting the ecological performance of macroalgae in real ecosystems. Although previous research has shown a linear increase in production with irradiance in simple assemblages on dense monocultures (Middleboe & Binzer 2004; Binzer & Middleboe 2005), my research shows a further increase in production at high irradiance within natural intertidal assemblages. The increase in complexity from single thalli to intact *in situ* assemblages shows a progression from a typical saturation curve to a linear P-E curve, to a unique two-stage curve (Fig. 8.1).

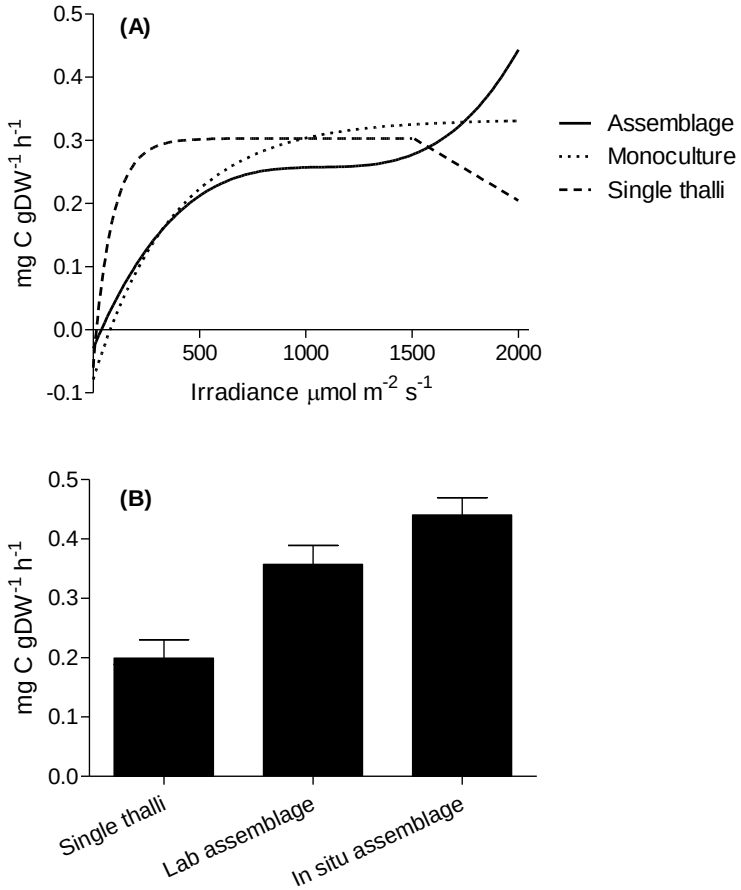

Figure 8.1. Stylised diagram of the effects of assemblage complexity on the relative shape of P-E curves. Including single thalli, monocultures, and multi-species assemblages (A), and the difference in production at high irradiance (2000 µmol m^{-2} s^{-1}) between treatments (B).

The shift in P-E curve shape with increasing assemblage complexity is also associated with a rise in production at high irradiance, but a fall in production at low irradiance (Fig. 8.1 A). At high irradiance there are large differences in production between all three methods, with *in situ* assemblages having the highest maximum production (Fig. 8.1 B). As assemblage structure increases and more natural variables are considered, these assemblages become more efficient at using light. However, this is also associated with increased competition for light at low irradiances in complex assemblages. This suggests a shift from competition to complementarity with increasing levels of the light resource. Only when irradiance reaches above the onset of photosaturation would canopy structure influence community production (Binzer & Sand-Jensen 2002b). Therefore, at low irradiance photosaturation of many components within the assemblage may not be reached, resulting in higher respiration rates in the lower canopy levels. At high irradiance levels the high density of algae results in an even distribution of photons and, therefore, an even absorption between assemblage components. If this is achieved, an increase in irradiance will not saturate photosynthesis at the tissue level and there will be an almost linear relationship between community photosynthesis and incident irradiance up to 2000 µmol m^{-2} s^{-1} (Ruimy et al. 1995). Results from this study are generally in agreement with this, but show a further rise at high irradiance as opposed to saturation. However, in the mid-range of irradiance there is a distinct plateau (between 500-1500 µmol m^{-2} s^{-1}) suggesting an uneven distribution of irradiance. If irradiance is unevenly distributed, most of the incident irradiance would be absorbed by the canopy plants or upper layers, resulting in saturation by the upper layers (Binzer & Middleboe 2005), as is observed throughout the mid range of irradiance. This suggests that above 1500 µmol m^{-2} s^{-1}, a critical threshold is crossed allowing the lower canopy levels to contribute more effectively to community production. At high irradiance the subcanopy assemblage adds significantly to the production of the whole community indicating an essential role of functional diversity.

The structure of plant communities has long been considered an important factor regulating whole community production, but up until recently, little had been done regarding the structure of aquatic autotrophic assemblages (Binzer & Sand-Jensen 2002a; Binzer & Sand-Jensen 2002b; Binzer & Middleboe 2004; Binzer & Middleboe 2005). These studies provide essential insight into the potential role of canopy structure and density in enhancing photosynthetic efficiency. Although diversity was considered by Middleboe & Binzer (2004), very little research has attempted to examine macroalgal

assemblages in their natural state. The predictable layering of many macroalgal assemblages (Reed & Foster 1984; Schiel 2006) must result in evolution or adaptation of photosynthetic strategies relative to the light environment where each species occurs. Therefore, production of intact natural assemblages may show the mechanisms underpinning the enhancement of production in diverse assemblages. This research shows that canopy structure and natural assemblage composition is essential to the way assemblages utilise light. The loss of canopy or subcanopy functional groups could have a large impact on total assemblage production through changes in the efficiency of light use.

8.3. Functional groups and species redundancy

Primary production of intertidal macroalgal assemblages appears to be particularly dependent on the canopy forming species, the loss of which causes a dramatic fall in total production. However, evidence from this study has shown that several canopy layers are responsible for overall assemblage production, particularly at high irradiance. The use of functional groups has often been used to describe the roles and responses of many species in multiple ecosystems (Naeem & Wright 2003). Marine macroalgae are characterised by a range of traits including competitive ability, resistance to herbivores, production, and nutrient uptake (Littler & Littler 1980). Furthermore, these functional groups can be composed of unrelated species, which share similar longevity, canopy height and production potential (Steneck & Dethier 1994). Using these attributes, the various species within these intertidal assemblages can be categorised into 4 functional groups. These are 1) the dominant canopy forming species i.e., *Hormosira banksii* or *Durvillaea antarctica*, 2) perennial subcanopy species i.e., *Cystophora torulosa* in the mid shore, 3) the basal turf or encrusting coralline species i.e., *Corallina officinalis*, and 4) the basal/subcanopy ephemeral species i.e., *Champia novae-zelandiae*, *Lophothamnion hirtum*, and *Colpomenia sinuosa*. The presence of functional redundancy within these functional groups would help buffer communities from species loss. The potential for redundancy in terms of potential replacement has been examined in these systems by Schiel (2006) and this study further examines potential for redundancy in terms of primary production.

Evidence from this study and from Schiel (2006) suggests that there is no functional equivalents for *H. banksii* in the mid shore, but in the low-shore *Cystophora torulosa* dominated zone, there may be the potential for functional replacement of the

canopy species. Although the recovery of production after the loss of *H. banksii* in the mid shore occurred only after recruitment of *H. banksii*, the recovery of production after the loss of *C. torulosa* was not associated with its recruitment back into the assemblage. Furthermore, the loss of canopy forming *C. torulosa* in the low shore, had a much smaller impact on assemblage production than the loss of *H. banksii* in the mid shore, suggesting increasing functional redundancy down a gradient of stress. The loss of *C. officinalis* is associated with an initial loss in production, but after 6 months, production had increased significantly, which was not associated with recruitment of *C. officinalis*. Although the loss of ephemeral species was not specifically tested in this study, these species varied significantly between plots and over time. This suggests that although this functional group is important to overall production at any given time, the actual species identity is trivial. However, the wide variation in life-histories of ephemeral algae may result in enhancement of production over time. Diversity in a given plot may be low at any one time, but the large diversity over time may enhance community production on an annual basis. Evidence shows that much of the diversity on these reefs is not perennial, with only fucoids and encrusting corallines occurring in macroscopic form throughout the year (Schiel 2006). The effects of species loss in these systems are likely to be idiosyncratic and related to the identity of the species lost with the canopy species acting as 'key species' in these systems.

Many studies suggest or report low functional redundancy in numerous ecosystems (Bellwood et al. 2003; Loreau 2004; Micheli & Halpern 2005; Schiel 2006). Research on the marine environment suggests very little redundancy in grazer assemblages (Duffy et al. 2001), coral reef fish assemblages (Bellwood et al 2003), temperate fish assemblages (Micheli & Halpern 2005) and temperate macroalgal assemblages (Schiel 2006). This research suggests much the same, particularly in regards to canopy forming macroalgae. However, there appears to be significant functional redundancy in the subcanopy macroalgal assemblage at any given time, but species diversity may be essential over longer temporal scales. Long-term grassland experiments indicate an essential role of biodiversity on ecosystem stability (Tilman et al. 2006), suggesting that species diversity can buffer any major perturbations to the system. It also appears that the presence of functional redundancy increases with decreasing physical stressors. Loss of canopy species has a much smaller impact on production in the low shore, suggesting a buffering capacity of the subcanopy species. The loss of canopy species in the mid shore is associated with a loss in biodiversity (Lilley & Schiel 2006)

and as seen in this study, a loss in production. This research gives valuable insight into the level of redundancy within intertidal macroalgal assemblages, and suggests that the assemblages most susceptible to species loss are those in areas of high physical stress. In these zones the canopy species play a vital role in habitat amelioration (Bertness et al. 1999; Lilley & Schiel 2006; Schiel 2006), the loss of which can have large effects on not only diversity, but on primary production. The loss of the key canopy forming species from the mid shore, is likely to have significant flow on consequences to the surrounding communities through changes in carbon export. Understanding the assemblages least resiliant to disturbance may provide essential guidelines to environmental agencies, and lead to the protection of fragile ecosystems.

8.4. Comparisons and contrasts with terrestrial systems

Comparisons between terrestrial and aquatic systems have estimated that aquatic systems are approximately 5 times less productive than terrestrial systems (Sand-Jensen & Krause-Jensen 1997). However, this is not the general consensus among comparative studies of primary production, with some studies placing marine macroalgae among the most productive systems on earth (Whittaker & Likens 1973). The apparent disparity between marine and terrestrial systems, indicates that phytoplankton, submerged macrovegetation and attached microalgae are all far less productive than terrestrial systems (Fig. 8.2). However, this study indicates that gross primary production of macroalgae (Fig. 8.3) is much higher than predicted by Sand-Jensen & Krause-Jensen (1997). The results from this study indicate that some macroalgal assemblages are well in line with terrestrial systems, and the disparity observed by Sand-Jensen & Krause-Jensen (1997) may be due to methods (i.e., single species as opposed to assemblage production) or associated with the particular systems examined.

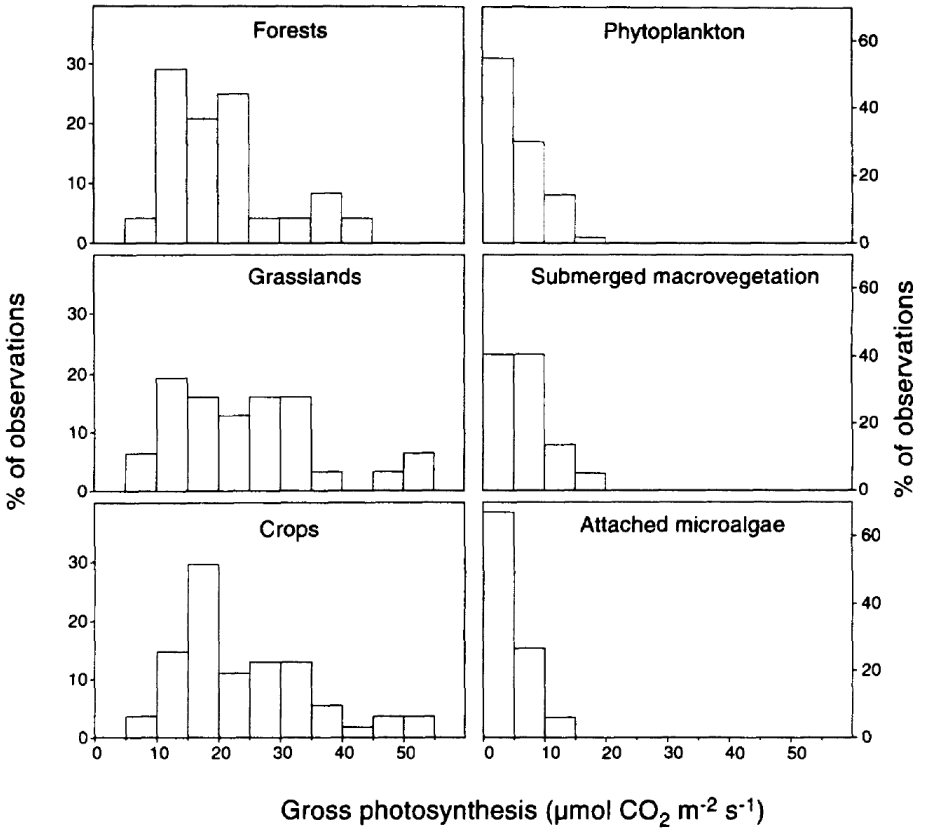

Figure 8.2. Percentage of observations of primary production (1000 µmol m^{-2} s^{-1}) at various ranges in terrestrial and aquatic systems (Figure from, Sand-Jensen & Krause-Jensen 1997).

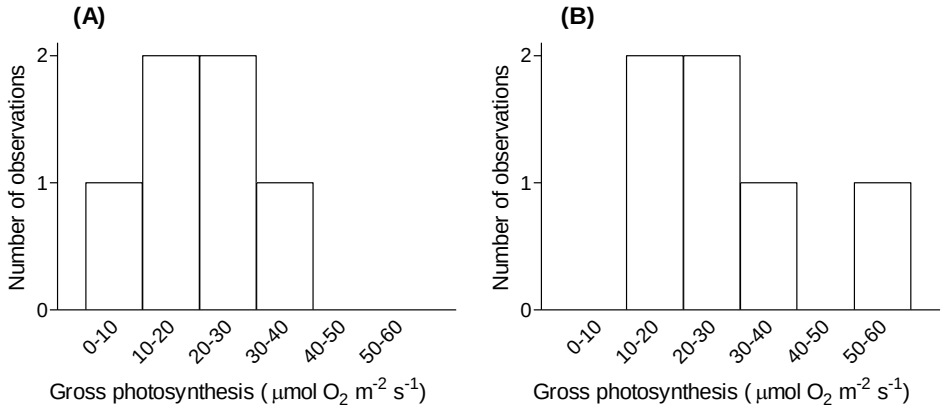

Figure 8.3. Number of observations of gross production within various ranges at (A) 1000 µmol m^{-2} s^{-1} and (B) 2000 µmol m^{-2} s^{-1}.

The disparity between terrestrial and aquatic ecosystems was suggested to be due to the rigid structure of terrestrial assemblages and the ability of plants to change leaf inclination in order to enhance incident irradiance to lower canopy levels (Sand-Jensen & Krause-Jensen 1997). Marine plants do not have the rigid structure to enable them to

orientate leaves favourably in respect to light interception (Binzer & Middleboe 2005), and the constant movement of thalli in the marine environment leads to a random distribution of light to lower canopy levels. However, this also has the potential to inhibit the role of competitive dominants, which under stable conditions could almost completely shade subcanopy plants. The high levels of canopy movement and unpredictable light source may help a myriad of species to persist in the subcanopy of marine macroalgal assemblages. This hypothesis is supported by evidence that there is no density-dependent mortality of some macroalgae and growth rates are actually enhanced at high densities (Schiel & Choat 1980). Furthermore, this study indicates that at high irradiance, there is complementary light use between all canopy components, suggests marine macroalgal assemblages are able to use light efficiently. This research suggests that there may, in fact, be some important similarities between terrestrial and marine ecosystems and this research may give some essential insight into the impacts of species loss on function across ecosystems.

The net primary production (NPP) of autotrophic ecosystems is essential to our understanding of global carbon budgets and has implications for climate change driven by anthropogenic release of greenhouse gases (Baldocchi et al. 2001). One of the major uncertainties in the determination of NPP in forest ecosystems has been the balance between NPP and heterotrophic respiration (Clark et al. 2001a). Due to difficulties in measuring below-ground plant respiration, this component is often estimated as a theoretical proportion of above-ground values (Clark et al. 2001a). However, calculations of NPP are much simpler in aquatic autotrophic assemblages through measurements of changes in dissolved gases. Furthermore, due to the relative lack of tissue specialisation, respiration and photosynthesis occur at almost all tissue levels. This makes estimations of NPP much simpler in aquatic macrophyte assemblages and has the potential to produce accurate estimates of energy budgets in these systems. Estimates of NPP on a global scale based on a number of studies suggest that terrestrial ecosystems can produce between 100-1500 g C m^{-2} yr^{-1} (Melillo et al. 1993; Cramer et al. 1999). NPP of the macroalgal assemblages tested in this study suggest an annual production between 700-5000 g C m^{-2} yr^{-1}. This difference could be caused by several factors, including: 1) an over-estimation of production in this study, 2) an underestimation of production in global models of terrestrial production, and 3) inherent differences between marine and terrestrial systems. First, is data from this study an overestimation of macroalgal production? Primary production of the assemblages measured in this study is very similar

to the production measured in a range of macroalgal and seagrass assemblages by other authors (Ferreira & Ramos 1989; Cambridge & Hocking 1997; Duarte & Ferriera 1997; Reed et al 2008; as seen in Chapter 7, Table 7.6). Furthermore, this study has several advantages over some of these studies (Ferreira & Ramos 1989; Cambridge & Hocking 1997), in that irradiance and production are measured *in situ* and production of whole assemblages, as opposed to single species, are considered. Furthermore, the intertidal zone is exposed to much higher irradiance than subtidal macroalgal and seagrass assemblages (Duarte & Ferriera 1997; Reed et al. 2008), potentially elevating production. The upper end of production in these macroalgal assemblages could be an overestimation of production, but given that Reed et al. (2008) estimate maximum production of *Macrocystis pyrifera* at 2400 g dry mass m^{-2} yr^{-1}, estimates from this study are potentially accurate.

The second factor potentially affecting comparisons between terrestrial and aquatic systems is the underestimation of terrestrial NPP. A comparison of the methods used for NPP estimation in forest ecosystems, suggest that it is largely underestimated (Clark et al. 2001a). Local scale estimates put the production of tropical forests between 1700-21000 g C m^{-2} yr^{-1}, much higher than previous estimates (Clark et al. 2001b). Their research suggests that large scale models may fail to accurately estimate local scale differences in production, and suggest that in certain systems, NPP may be largely underestimated. The last potential reason for differences between terrestrial and aquatic models is that there are inherent differences between the two systems. This has already been largely addressed (see above), with the biggest difference being the need to understand above- and below-ground processes in terrestrial systems, but not in aquatic systems. Overall, despite the large perceived differences between marine and terrestrial systems, there may in-fact be a large overlap in the relative production of both systems, and therefore, findings on the dynamics of production from one system have the potential to be relevant for other autotrophic assemblages.

8.5. Implications for Biodiversity-Ecosystem Function research

Although biodiversity-ecosystem function research is expanding in the marine environment, certain systems have received more attention than others. In particular, soft sediment systems have been extensively studied (Emmerson et al. 2001; Solan et al. 2004; Bremner 2008), including seagrass beds (Duffy et al. 2001). Several studies have

attempted to test the impacts of biodiversity loss on ecosystem function in rocky shore systems (Bruno et al 2005; Schiel 2006; Stachowicz et al 2008), and only a handful have examined the effects of macroalgal diversity on production (Bruno et al 2005; Griffin et al. 2009), or proxies for production (Bracken et al. 2008). Overall, macroalgal systems have been largely neglected in the biodiversity-ecosystem function (BEF) literature. Results from Bruno et al. (2005), show similar patterns and processes as have been observed in the terrestrial literature, with a general positive influence of diversity on production, but with selection effects outweighing complementarity effects. However, research on macroalgae has the potential to give insight into BEF research beyond general comparisons with other systems. First, many difficulties in the interpretation of results from terrestrial plant assemblages are associated with differences in below-ground nutrient use and above-ground light use (Vojtech et al. 2008). Macroalgal assemblages have no true root systems, and are bathed in the surrounding medium, with nutrient uptake occurring at all tissue levels by diffusion. Second, the simultaneous competition for below-ground nutrients and above-ground light can easily complicate interpretation of primary production results which is often measured as changing biomass (Tilman & Downing 1994). Because change in biomass is the consequence of a myriad of processes integrated over relatively long time scales, determining the factors driving production can be difficult. Third, the relatively small size of many macroalgal assemblages and the properties of water make it easy to examine physiological primary production of whole assemblages on relatively short time-scales. This has facilitated research on the function of light in whole assemblages and the potential for complementary light use. Although results from macroalgae are not necessarily transferable to other autotrophic assemblages, they do indicate the potential for similar mechanisms to occur within other systems.

As well as the potential for complementary light use to enhance production, this study shows that non-random species losses have the potential to develop our understanding of how species loss might impact ecosystem function. Since extinction or loss of species is a non-random process (Naeem 2006), it is intuitive that the effects of species loss are likely to be non-random. The loss of canopy species, those most prone to loss or damage (Lilley & Schiel 2006; Schiel 2006), has large consequences on the production of macroalgal assemblages. This is on top of the impacts that canopy loss has on community composition through niche expansion (Bertness et al. 1999; Bruno et al. 2003). Furthermore, the cascading effects of canopy loss on community composition causes a severe reduction in primary production. Although the loss of the subcanopy and

basal species causes a decline in assemblage production, the loss of the canopy causes by far the greatest fall in production (see chapter 4). Loss of canopy species has the potential to severely affect production of macroalgal assemblages, with large scale disturbances potentially impacting biomass output on the ecosystem scale. Furthermore, the potential negative feedback in fucoid recruitment from coralline turfs has the potential to reduce primary production for periods exceeding 2 years in certain areas (see chapter 6). The loss of these 'key' species has the potential to impact ecosystem wide production and could have wide reaching consequences to higher trophic levels. This research shows unequivocally that these canopy forming fucoids are essential to the functioning of these near shore ecosystems and given the relative lack of subtidal reefs in large areas of New Zealand's South Island, may be vital to the functioning of large stretches of the coastline with their influence potentially spreading to offshore areas.

8.6. Conclusions

Despite the considerable interest and the high number of publications on primary production, relatively few studies have attempted to define production of macroalgal assemblages on large scales since some of the pioneering studies (Mann 1973; Jackson 1977; Littler & Littler 1980). Evidence from the terrestrial literature suggests that despite great advances in techniques and technology, there are several largely un-answered questions in relation to the factors influencing production on large scales (Clark et al. 2001a & b). Intuitively, one would expect the same to be true for marine systems, yet very little research on ecosystem-scale, macroalgal production has been done, with the notable exception of Reed et al. (2008). This research represents several advances in measuring production of macroalgal assemblages. These include 1) the development of an apparatus able to measure primary production of *in situ* macroalgal assemblages and the ability to re-visit the same macroalgal assemblages; 2) showing the importance of assemblage structure and species diversity in overall net primary production; 3) the development of a model able to predict primary production across whole reefs using *in situ* irradiance and *in situ* carbon fixation. This research gives valuable insight into the production of marine macroalgae and reinforces the notion that they are amongst the most productive systems on earth. Hopefully, this study will give impetus to further research on macroalgal assemblages, particularly an understanding of how much biomass is lost to surrounding systems, and where it is exported to.

This research helps our fundamental understanding of how macroalgal assemblages use resources such as light, and also shows the importance of inter-species interactions. This shows that the typical saturation curve used for single thalli is not representative of whole assemblages in high light environments, and therefore, studies using primary production as a proxy for 'ecosystem function' need to take irradiance into consideration, as opposed to assuming a saturating irradiance. Evidence from this study shows that the role of biodiversity in the enhancement of production is linked to resource levels, and testing function at only one level of irradiance may lead to inaccurate conclusions. The essential role of irradiance and assemblage structure shows the high level of complementarity in real systems and shows the benefits of research on real assemblages compared to randomised assemblages or laboratory- mesocosm- based experiments.

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Appendix I. Effects of time on reduction in productivity in a sealed incubation chamber (From Figure 3.5, Chapter 3).

Table 1. Bonferroni post-hoc test comparisons between two levels of irradiance (µmol m^{-2} s^{-1}) at various times after the sealing of incubation chambers.

Comparisons	1000-800		1200-800		1200-1000		2000-800		1000-2000		1200-2000	
Time	t	p	t	p	t	p	t	p	t	p	t	p
20	-	ns	3.8	<0.01	4.2	<0.001	16.5	<0.001	16.9	<0.001	12.6	<0.001
40	-	ns	4.7	<0.001	3.7	<0.01	19	<0.001	18	<0.001	14.3	<0.001
60	-	ns	-	ns	-	ns	6.8	<0.001	7	<0.001	6.4	<0.001
80	-	ns	-	ns	-	ns	-	ns	-	ns		ns

Appendix II. Raw *in situ* irradiance data beneath canopy of *Hormosira banksii* (Chapter 4).

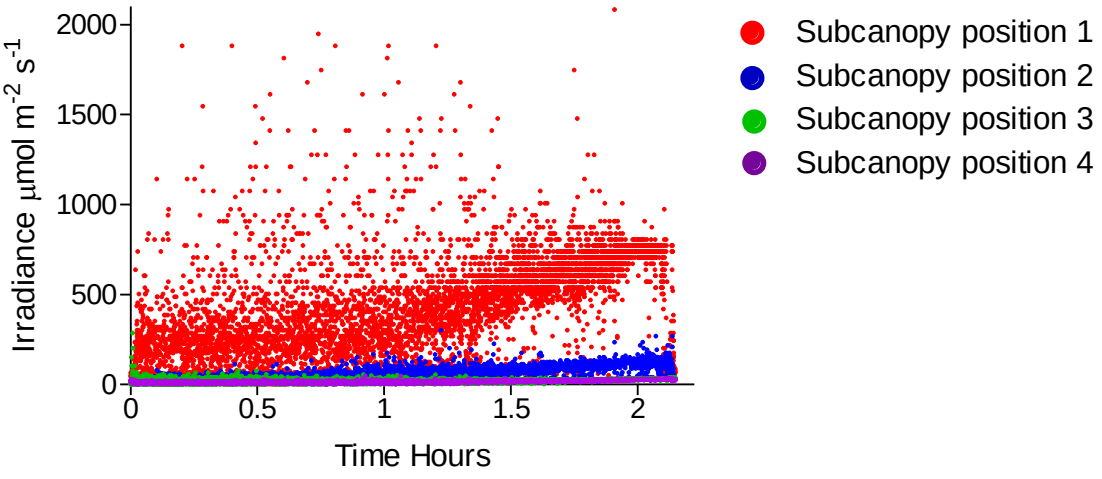

Figure 1. Subcanopy irradiance at 4 positions surrounding an *Hormosira banksii* assemblage.

Appendix III. Univariate and multivariate graphs of multi-factor ANOVA Table 5.5 and Fig. 5.18 (Chapter 5).

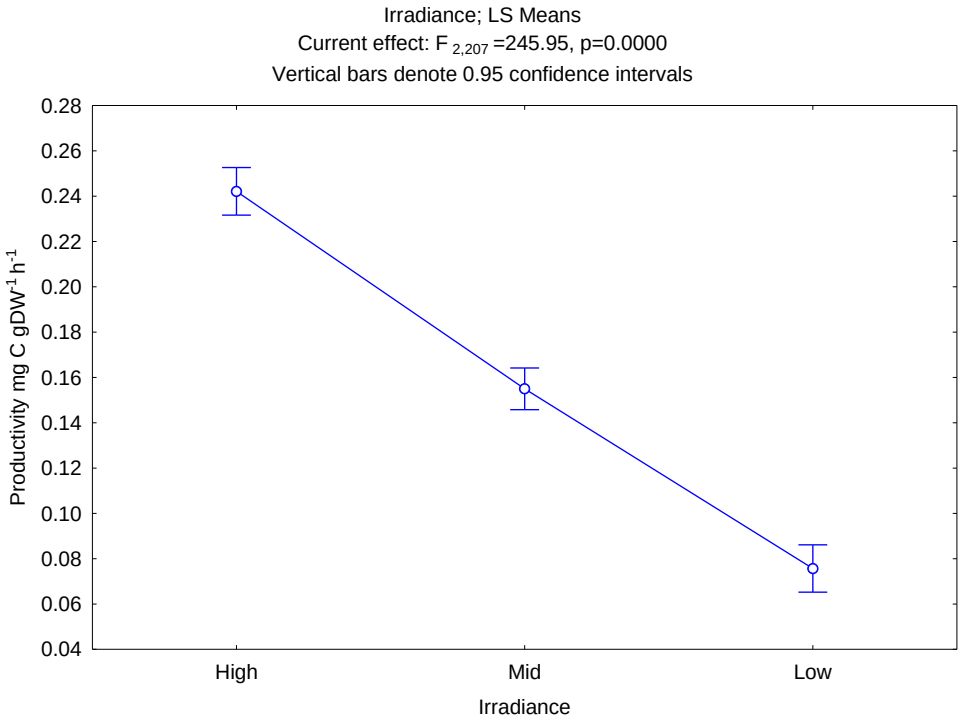

Figure 2. Univariate analysis of the effects of irradiance on productivity using factorial ANOVA.

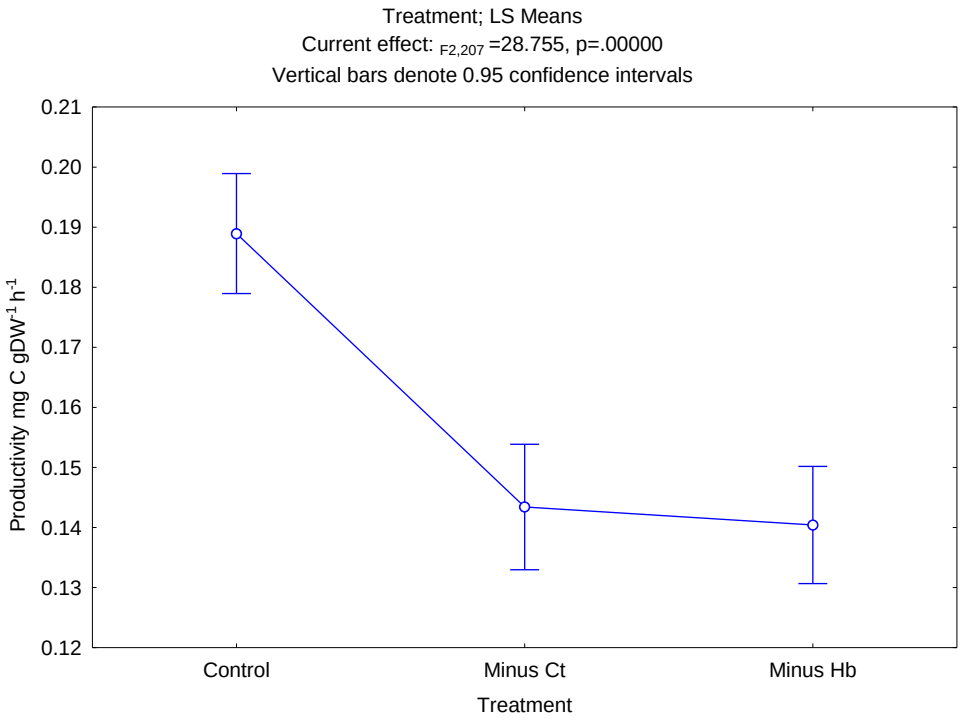

Figure 3. Univariate analysis of the effects of treatments on productivity using factorial ANOVA.

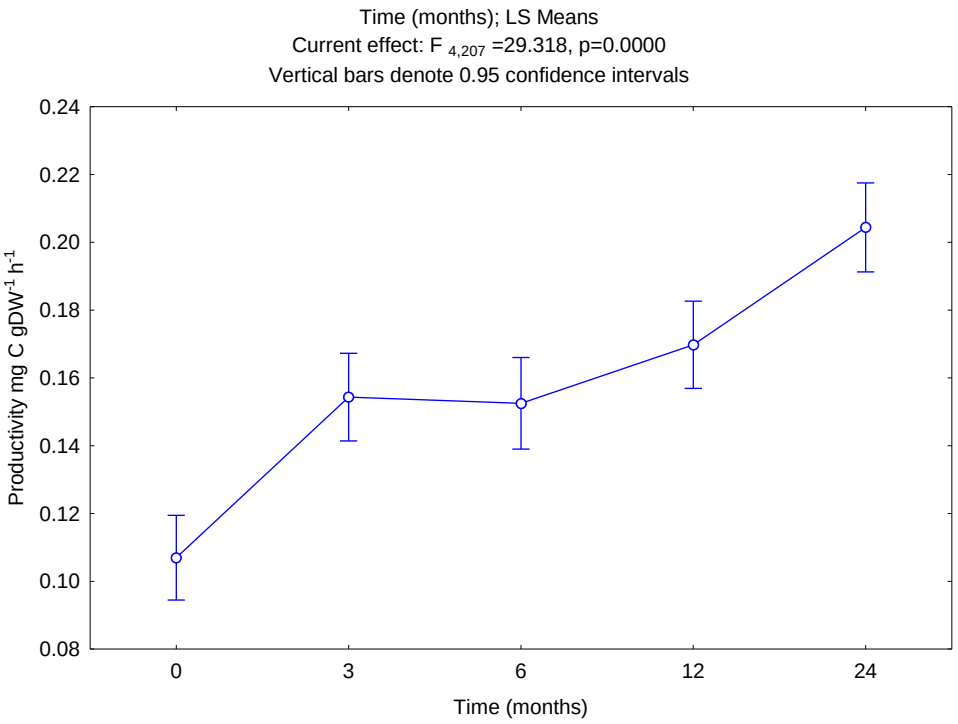

Figure 4. Univariate analysis of the effects of time on productivity using factorial ANOVA.

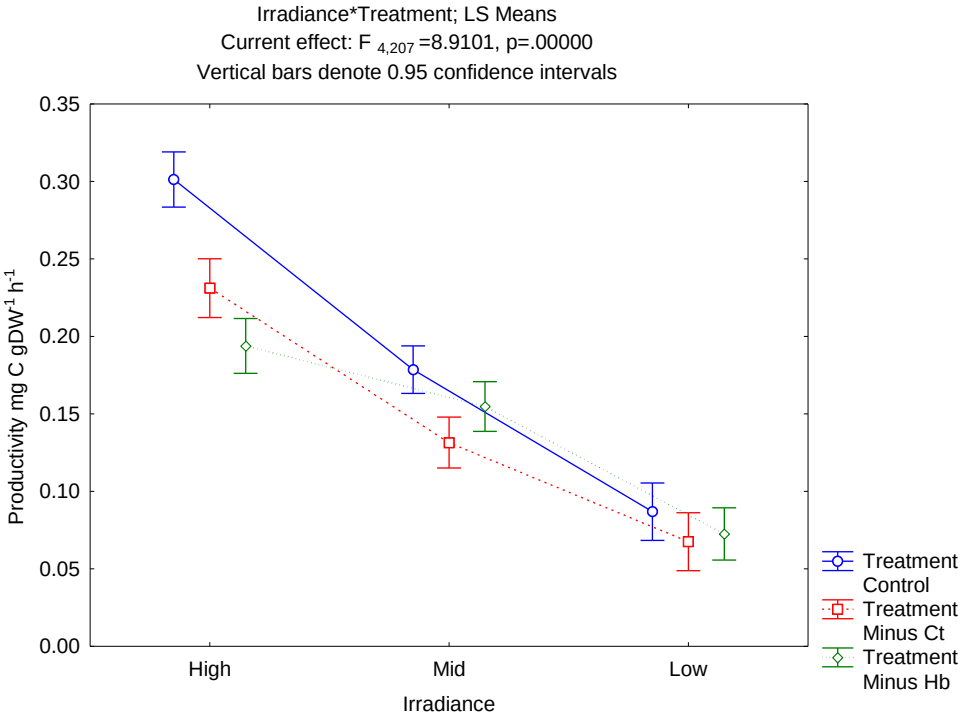

Figure 5. Interaction effects of irradiance and treatment on productivity.

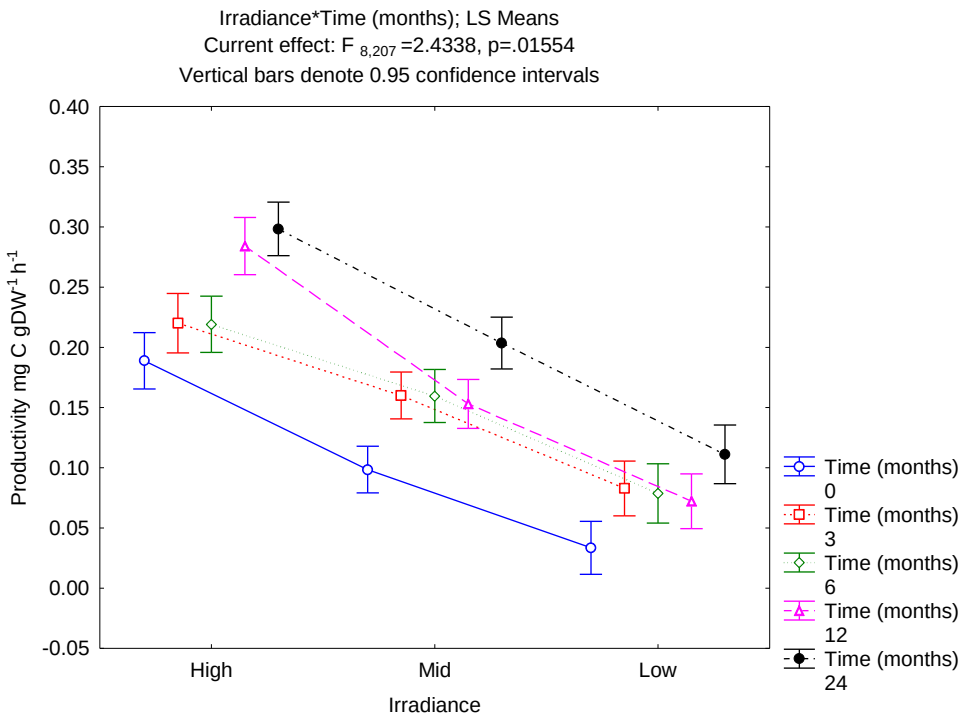

Figure 6. Interaction effects of irradiance and time on productivity.

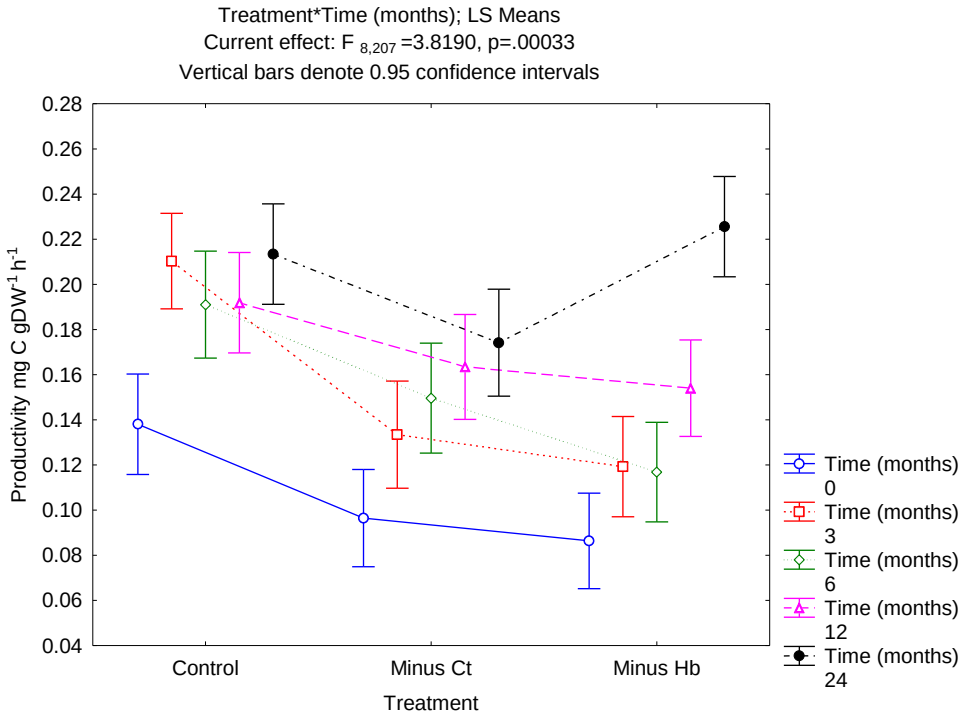

Figure 7. Interactive effects of treatment and time on productivity.

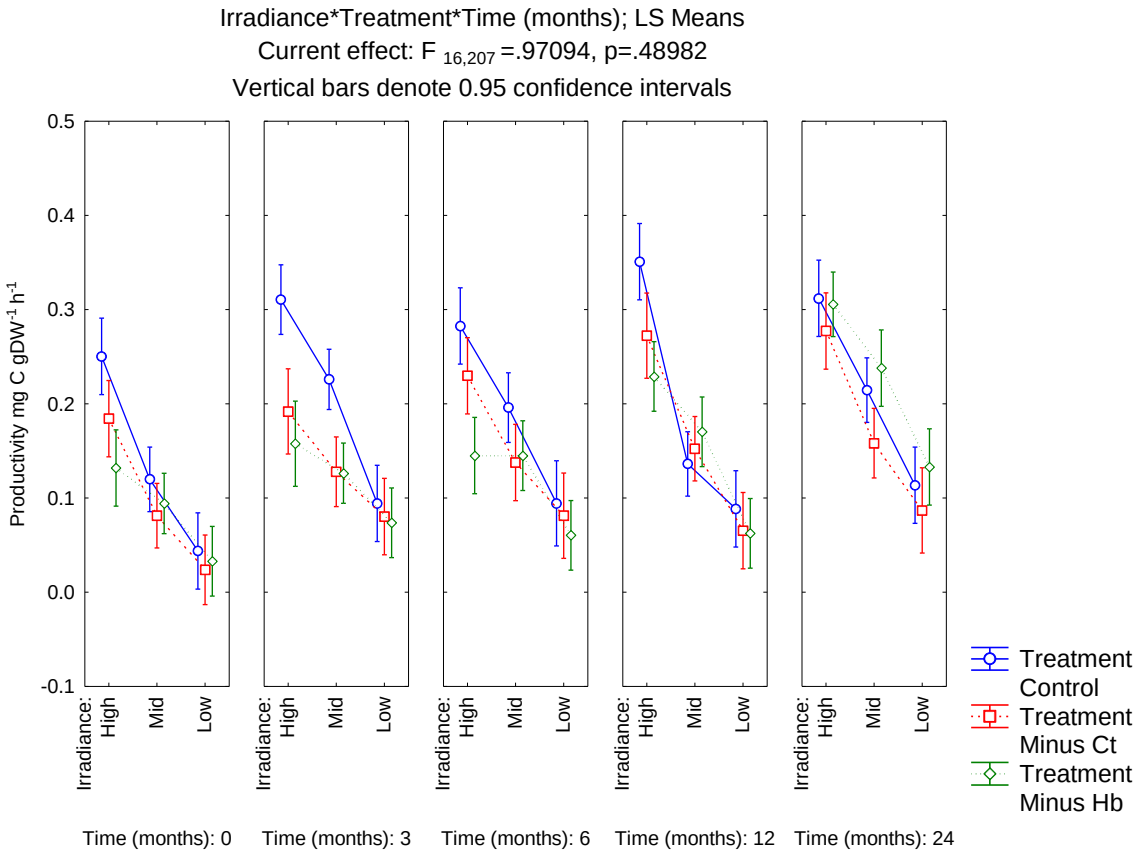

Figure 8. Effects of three-way interation between irradiance, treatment and time on productivity.